DISSERTATION

WILDLIFE COMMUNITY OCCURRENCE, ACTIVITY PATTERNS, AND INTERSPECIFIC INTERACTIONS IN RESPONSE TO ENERGY DEVELOPMENT

Submitted by

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ABSTRACT

WILDLIFE COMMUNITY OCCURRENCE, ACTIVITY PATTERNS, AND INTERSPECIFIC INTERACTIONS IN RESPONSE TO ENERGY DEVELOPMENT

Energy extraction is one of the primary drivers of land use change in North America, particularly oil and gas development, which is projected to increase by 40% over the next 20 years. Such human-mediated landscape changes can have direct affects to wildlife including impeding or disrupting movement patterns, decreasing habitat suitability, changing individual behaviors, and altering population and community structure. Carnivores, which are vital to a healthy ecosystem, are thought to be particularly vulnerable to habitat modifications because of their naturally occurring low densities, large ranges, and aversion to areas with high human activity. My dissertation focused on the distribution of the carnivore community and their prey in relation to energy extraction features in the Piceance Basin of northwest Colorado, one of the largest natural-gas reserves in North America.

The effects of anthropogenic disturbance on predator-prey relationships are fundamental to ecology, yet less well understood. Therefore, in Chapter 1, we investigated the relationship between predation sites, energy infrastructure, and natural landscape features across contiguous areas experiencing different degrees of energy extraction during periods of high and low intensity development. We determined where predation events occurred for fawn and adult female mule deer from 2008–2014 in critical winter range with extensive energy development. We contrast spatial correlates of 286 mortality locations with random landscape locations and mule deer distribution estimated from 350,000 GPS locations. We estimated predation risk with

resource selection functions and latent selection difference functions. Relative to the distribution of mule deer, predation risk was lower closer to pipelines and well pads, but higher closer to roads. Predation sites occurred more than expected relative to availability and deer distribution in deeper snow and non-forested habitats. Anthropogenic features had a greater influence on predation sites during the period of low activity than high activity, and natural landscape characteristics had weaker effects relative to anthropogenic features throughout the study. Though canids accounted for the majority of predation events, felids exhibited stronger landscape associations, driving the observed spatial patterns in predation risk to mule deer. The emergence of varied interactions between predation and landscape features across contexts and years highlights the complexity of interspecific interactions in highly modified landscapes.

Assessing the degree to which animals behaviorally respond post disturbance can also help identify activities of concern or populations at risk. In chapter 2, we examined circadian activity patterns of bobcats, coyotes, mule deer, elk, lagomorphs, and rodents during crepuscular, day, and night periods using data captured from 40 remote cameras distributed across a 162 km^2 area with starkly different levels of current and historical energy development. During the winter of 2015-2016, we obtained 3,067 independent detections from 7,185 camera days of our six target species. In mixed support of our hypotheses, bobcats, coyotes, and mule deer were less active during the day in the developed site compared to the undeveloped site, as were rodents which was unexpected. In contrast, elk and lagomorphs did not show differences across sites. Bobcats demonstrated the greatest reduction in diurnal activity, with nearly three times less activity in the developed site. Coyotes and mule deer appeared to compensate for reduced activity during the day by increasing their activity during other periods, though bobcats did not. The mammal species captured in this study demonstrated strong differentiation in their plasticity

and sensitivity to energy development approximately four years post high-intensity disturbance, which likely influences their susceptibility to human-driven landscape changes.

In Chapter 3, we examined the effects of energy development on carnivore communities occurrence from 2014-2017. With data collected from 80 remote triggered cameras across a ~300 km^2 area, we estimated cougar, bobcat, and coyote habitat use with single-species multiseason occupancy modeling. Top models indicated a higher occurrence of bobcats and coyotes at low well pad densities, though there was large uncertainty in our estimates at high well pad densities. Coyote occurrence was higher in low elevation areas, and bobcats had a greater probability of occurrence in woodland than in shrub covered camera stations. Across seasons, coyote occurrence and probability of detection were high and 1.5 and 2 times that of bobcats, respectively. The occurrence of bobcats was comparable to that observed in exurban development, but lower than in populations that experience little human persecution. Only two detections of cougars were obtained across the three winter seasons, preventing occupancy estimation. The region is predicted as having the potential for high cougar densities based on habitat quality, but is managed for moderate suppression. The management objective combined with the high road densities associated with energy development increasing hunter access likely accounted or the low cougar occurrence observed. Our results suggest changes in habitat use correlated with energy development persist during the production phase, a phase when ecological impacts are assumed to be ameliorated and has the longest tenure on the landscape. Information regarding the influence of production phase energy development on carnivore habitat use can provide important information for wildlife conservation and aid in science-based management decisions.

Given the strong predatory role of humans in most systems, human presence or disturbances often are perceived as predatory pressures, even to predators themselves, which can drive alterations in species interactions and habitat use related to anthropogenic features and activities. Foraging theory predicts that animals should spend less time in habitats associated with greater risk if adequate resources are available in less risky environments. In Chapter 4, we used multispecies occupancy modeling to examine if anthropogenic disturbance in the form of energy development acted as a type of predation risk and altered patterns of species co-occurrence for a specialist (bobcat) and generalist (coyote) predator and their primary prey (rabbits) in contrasting periods of high and low relative rabbit abundance. We hypothesized that these mesocarnivores would exhibit risk-sensitive habitat use in the presence of energy infrastructure, and that bobcats would be more sensitive than coyotes because of their specialized behaviors. When relative rabbit abundance was high, bobcats displayed less probability of use at sites with high well pad densities, consistent with the risk-averse, but switched to risk-prone behavior when rabbit abundance was low, displaying a relatively equal probability of use across all well pad densities. Coyotes appeared to be less displaced, occurring across the gradient of disturbance regardless of relative rabbit abundance, though greater uncertainty in estimates existed at higher well pad densities. Our results support the specialist-disturbance hypothesis that posits specialist species are more likely than generalists to alter habitat use in response to human disturbance. Furthermore, reductions in prey availability may increasing the possibility for human-wildlife interactions by species that would otherwise avoid human-disturbed habitats. As conservation practitioners prepare for greater human-induced habitat alteration and changing environmental conditions, the combined use of theoretical ecology and empirical studies can inform conservation efforts.

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CHAPTER ONE

PREDATION RISK ACROSS A DYNAMIC LANDSCAPE: EFFECTS OF ANTHROPOGENIC LAND USE, NATURAL LANDSCAPE FEATURES, AND PREY DISTRIBUTION

INTRODUCTION

Natural and anthropogenic disturbances affect community assembly through alterations in habitat conditions (Larsen and Ormerod 2014). Humans are the primary drivers of contemporary habitat loss and degradation, with strong effects on community structuring and interactions (Wilcove et al. 1998; Chapin et al. 2000). The effects of habitat loss can be direct, via the destruction or alteration of habitat, or indirect, for example via behaviorally driven avoidance of human activities (Frid and Dill 2002) resulting in functional habitat loss (Aldridge and Boyce 2007). The potential for indirect impacts is emerging as a major concern given increasing anthropogenic development globally and potential effects on wildlife populations (Leu et al. 2008).

Habitat loss affects 40 percent of the world's mammals (Schipper et al. 2008). Of these species, carnivores are thought to be particularly vulnerable to habitat alteration because of their relatively large ranges, low numbers, and direct persecution by humans (Crooks 2002). In addition to direct displacement by disturbance, prey abundance and distribution are also key drivers of demography and distribution of large carnivores (Carbone and Gittleman 2002; Karanth et al. 2004). Ungulates are the primary prey base for many large carnivores throughout the world, including the western United States (Hurley et al. 2011; Elbroch et al. 2013). Prey species must make trade-offs between resource acquisition and risk of mortality, whether the risk

is real or perceived (Frid and Dill 2002), and may do so by altering their spatio-temporal patterns of habitat use (Laberee et al. 2014). A growing number of studies have observed avoidance of human-caused disturbance by ungulates at large spatial scales (Northrup and Wittemyer 2013), while others have detected selection for areas of disturbance at finer scales (Berger 2007; Rogala 2011).

Variable responses of prey species to human disturbance could drive complex interactions between carnivores and disturbance. Because the effects of habitat change on carnivores may be mediated through the response of their prey (Burton et al. 2012), a better understanding of how predator-prey interactions are structured in human-altered landscapes is warranted. Traditionally, researchers have examined the location of predation events relative to the availability of landscape features (Husseman et al. 2003; Elbroch et al. 2013) or how prey distributions shape predation risk (Hebblewhite et al. 2005; Courbin et al. 2013). However, less is known about the combined influence of habitat characteristics and prey distribution on predation risk in multi-predator communities, despite the importance of such interactions in structuring ecological communities (Ford et al. 2014; Moll et al. 2017).

Across much of the western United States, sagebrush ecotones provide critical winter range habitat for mule deer, a principal big game species that has decreased across much of its range (Unsworth et al. 1999), in part from habitat loss and degradation resulting in reduced mule deer recruitment (Johnson et al 2016). These landscapes have been extensively developed for energy extraction (McDonald et al. 2009; Northrup et al. 2015), which influences mule deer distribution and habitat selection (Sawyer et al. 2006; Lendrum et al. 2012). The Piceance Basin in northwest Colorado, USA, contains the second largest natural-gas reserve in the country (Hawkins et al. 2016). The ongoing development continues to fragment the landscape with well

pads, pipelines, roads, and industrial facilities, which once supported one of the largest migratory mule deer herds across their range (Lendrum et al. 2014). We compiled a six-year data set of mortality events and mule deer space use across critical winter range habitat of the Piceance Basin to better understand how anthropogenic disturbance interacts with landscape characteristics and prey distribution to influence predation risk of mule deer.

Our primary objectives were to: (1) investigate mortality locations of radio-collared mule deer to determine cause-specific mortality and identify when and where predation occurred; and (2) evaluate the influence of anthropogenic disturbance on predation risk. For the latter objective, we examined the effects of landscape features on predation using resource selection functions (RSF; Boyce 2006) and the interaction between prey distribution and landscape features on predation using latent selection difference functions (LSDF; Erickson et al. 2014). We compared two contiguous areas with markedly different degrees of energy extraction that included a low intensity natural-gas development area ("undeveloped") and a relatively high intensity development area ("developed"), across two time periods representing different levels of active development, 2009-2011 ("high activity") and 2012-2014 ("low activity"). We hypothesized that: (1) during the high activity period, predation risk would be reduced in proximity to anthropogenic features with high levels of human activity (well pads and industrial facilities) because predators tend to be more adversely affected by human disturbance than prey (Berger 2007; Ripple et al. 2014), and that these effects would be reduced during the low activity period when human activity was reduced; and (2) predation risk would be increased in proximity to linear features (roads and pipelines) because linear features can facilitate the movement of predators (Leblond et al. 2013) and create edge habitat known to increase the risk of predation (Elbroch et al. 2013).

METHODS

Study Area

We monitored mule deer across varying levels of natural-gas development within the Piceance Basin (Figure 1.1): a developed area comprised of two subsections (141 km^2, 0.6 well pads/km^2 and 83 km^2, 0.8 well pads/km^2) and an undeveloped subsection (79 km^2, 0.1well pads/km^2; Lendrum et al. 2012, 2013). The climate of the region was typified by warm dry summers and cold winters, with most annual moisture in the form of winter snow and monsoonal spring rainstorms. The study area was topographically variable, with elevation ranging from 1,675 to 2,285 m. Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) were the dominant overstory species; common shrubs included big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Crysothamnus* spp.; Lendrum et al. 2014). Species of large carnivores included coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*). In addition to mule deer, the area contained other potential prey items including North American elk (*Cervus elaphus*), cottontail rabbits (*Sylvilagus* spp), as well as smaller rodents and birds.

Data Collection

From 2008-2014, mule deer were net-gunned from helicopters (Krausman et al. 1985). Three hundred-ninety adult female mule deer were captured and equipped with GPS collars (GPS-4400S, Lotek Wireless, Newmarket, Ontario, Canada, on 14 individuals the first year; G2110D, Advanced Telemetry Systems, Isanti, Minnesota, USA, thereafter). During the same time period, we also fit mule deer fawns (December captures annually; 6 months old of either sex) with VHF collars to monitor cause-specific mortality. Because carnivores are typically most active during crepuscular and nighttime hours in disturbed landscapes (Lendrum et al. 2017), and therefore

prey are most likely to be killed during these times (Anderson and Lindzey 2003), we only retained GPS locations that occurred between 18:00 and 06:00 in our analysis (see below). We stratified the dataset into 63,804 locations during the high activity period (2012-14) and 135,620 locations during the low activity period (2009-11) in the undeveloped area, and 78,066 locations during the high activity period and 127,255 locations during the low activity period in the developed area. GPS collars were store-on-board and programmed to attempt a fix once every 5 hours, with a subset of collars programed to obtained 1 hr fixes (Northrup et al. 2015). Collars were either programmed to drop off during April of the year following deployment (i.e., 16 months post capture) to allow collar retrieval and download of stored GPS locations, or January of the next year (i.e., 13 months post capture). Fawn collars were spliced and fitted with rubber surgical tubing to allow for growth and for collars to drop off between mid-summer and early autumn.

All collars were equipped with mortality sensors that transmitted a signal after 8 hrs of inactivity. A trained technician scanned for mortality beacons daily and investigated the site to determine cause of death after each mortality detection. Located carcasses were examined for hemorrhaging or peticiations to verify that a predation event took place rather than scavenging after a non-predation mortality (Stonehouse et al. 2016). To determine the predator involved, the width of the canine punctures, tracks present, and style in which carcass remains were distributed (i.e., cached or scattered) were recorded. If the predator was indiscernible, the predation event was marked as unknown predator, and if there was uncertainty if a predation event took place, the mortality was excluded from this analysis (Table 1.1). We compared predator-specific predation events with a non-parametric cumulative incidence function estimator for cause-

specific rates of mortality by age class of mule deer (Heisey and Patterson 2006). Descriptive statistics comparing predation sites, GPS, and random locations can be viewed in Appendix 1.1.

At each predation, GPS, and random location, we sampled four natural landscape variables known to influence predation risk (Hebblewhite 2005; Elbroch et al. 2013) and six metrics of anthropogenic disturbance previously identified to be influential in mule deer habitat selection (Sawyer et al. 2006; Lendrum et al. 2013; Northrup et al. 2015). Natural landscape variables included terrain ruggedness, distance to ecotone edge (forest and shrublands), concealment cover, and snow depth. Anthropogenic landscape features included distance to nearest well pad (producing and drilling), road (primary and secondary), pipeline, and industrial facility (Figure 1.1). Industrial facilities include compressor stations and operation centers of frequent human activity. Drilling well pads and industrial facilities occurred with such low frequency in the undeveloped site that these metrics of anthropogenic disturbance were retained in the model to control for variation, rather than make biological inference. A terrain ruggedness index was derived from a digital-elevation model (DEM) at a resolution of 30 m (http://datagateway.nrcs.usda.gov/) following the method of Sappington et al. (2007), ranging between 0 (flat) and 1 (most rugged). We reclassified the 87 vegetation classes provided by the Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/) layer, at a resolution of 25 m, into three broad categories of concealment based on similarity of vegetation types: (1) forbs, grasslands, and barren habitat types (low concealment); (2) shrub dominant (moderate concealment); and (3) forested habitats (high concealment). Snow depth was predicted for each day of the study at a resolution of 30 m from a distributed snow evolution model (SnowModel; Liston and Elder 2006). Variable inputs required for SnowModel include temporally varying fields of precipitation, wind speed and direction, air temperature, and relative

humidity obtained from meteorological stations and an atmospheric model located within or near the simulation domain; and spatially distributed fields of topography and vegetation type. Represented processes include accumulation from snow precipitation; blowing-snow redistribution and sublimation; interception, unloading, and sublimation within forest canopies; snow-density evolution; and snowpack ripening and melt (Liston and Elder 2006). Locations of well pads and industrial facilities were obtained from the Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/) from Dec 2008 – August 2014, which designated the date and location that each well pad was in a development (actively being prepared and drilled) or production (post drilling and actively extracting natural gas) phase (see Northrup et al. 2015 for further details). A roads layer was derived by combining the TIGER/Line shape files of the U.S. Census Bureau (http://www.census.gov/geo/www/tiger/shp.html) and the Colorado Department of Transportation shape files (http://apps.coloradodot.info/dataaccess/). We considered county roads as primary roads and spur roads used for purposes of natural-gas extraction as secondary roads, but we were unable to differentiate levels of vehicle use among roads. Locations of pipelines were obtained from the Bureau of Land Management White River field office. The spatial and temporal information for all landscape disturbances were validated or corrected with National Agriculture Imagery Program aerial images (http://datagateway.nrcs.usda.gov/) from 2009, 2011, and 2013.

Data Analysis

The landscape context of predation sites was examined using a generalized resource selection function approach (RSF; Manly et al. 2002; Boyce 2006). Natural (topographic, environmental, and habitat characteristics) and anthropogenic (proximity to energy development) features associated with predation sites were compared to an available sample drawn from within a winter

range area characterized by merging 1.2-km radius buffers around every predation location (approximately equivalent to the 4.5 km^2 average home range of deer in the system as described in Northrup et al. 2016). The relationship between predation sites and mule deer distribution (assessed from GPS telemetry data) was examined using a latent selection difference function (LSDF; Erickson et al. 2014), an analytical framework similar to resource selection functions used to provide quantitative estimates of differences in selection behavior between two datasets comprised of animal locations, in this case predation sites and GPS telemetered locations. All GPS locations within the buffer from the corresponding time frame were included in the LSDF analyses, and the sample of random locations employed in the RSF was set to the same number of GPS locations used in the LSDF to ensure comparability (Northrup et al. 2013). We first fit a macro-scale model that included only known canid (coyote) and felid (bobcat and cougar) predation locations across all study sites and years to determine how different hunting strategies (cursorial and ambush) might influence predation risk. We then pooled all kill sites regardless of predator species (providing insight to general predation risk) and fit separate models for spatial areas representing the undeveloped and developed sites, as well as across the two time periods of high and low energy development activity, resulting in 4 models (undeveloped low activity, undeveloped high activity, developed low activity and developed high activity).

We conducted separate RSF and LSDF models using a Bayesian logistic regression (Gelman and Hill 2006) framework run in the R statistical software (R Development Core Team, 2015) for each period of activity and level of development. The first 50,000 iterations of the Markov chain Monte Carlo (MCMC) algorithm written in R were discarded, and 500,000 samples were saved to build posterior distributions. To facilitate convergence and to allow for comparison of the magnitude of the effects of regression coefficients, we standardized

continuous predictor variables by subtracting their means and dividing by their standard deviations, but did not transform binary predictors (Gelman and Hill 2006). Standardization was also conducted using the mean and standard deviation calculated for all datasets combined to allow direct comparison of coefficients across time periods and study areas. Prior to fitting models, we tested for pairwise correlations among covariates to ensure that no covariates were highly correlated ($|r| > 0.7$) and calculated condition numbers to test for multicollinearity as suggested by Lazaridis (2007) to ensure that none were over 5.4.

We ran each MCMC algorithm twice for each model, using starting values that were expected to be overdispersed relative to the posterior distributions. Model convergence was evaluated by visual inspection of trace plots and by Gelman-Rubin diagnostic (mean values <1.1 indicate convergence; Gelman and Rubin 1992). With both analytical methods, the influence of a given feature on the location of a predation site can be interpreted by the directionality and magnitude of the median estimate of the coefficient. These relationships are multifaceted and vary depending on the variable being measured and therefore must be interpreted on a case-by-case basis (Appendix 1.2). If $\geq 90\%$ of the posterior distributions for the standardized β coefficients did not overlap zero, we concluded that there was strong evidence of an effect of the predictor variable. The magnitude of the coefficients allowed us to make inference about the relative influence of the given variable on the probability of a predation event occurring (Hobbs and Hooten 2015).

RESULTS

We radio-collared and monitored 1,357 individual mule deer including 126 adult female mule deer in the undeveloped study area and 264 in the developed area, and 316 fawns in the

undeveloped study area and 651 in the developed area. We documented 313 mortality events across designated winter range habitat (Table 1.1). Of these mortalities, we identified 286 as predation events, 22 as road kill, 1 hunter harvest, and 4 attributed to malnutrition or disease. One hundred fifty-three (53.50%) of the predation events occurred in the undeveloped study area and 133 (46.50%) occurred in the developed area.

Two hundred twenty-four predation events were of ≥ 6 month old fawns, constituting the majority (78.32%) of the depredated individuals, and 62 predation events were of adult females. Median overwinter predation rate of fawns and adult collared females was 0.18 (SE = 0.06) and 0.10 (SE = 0.01), respectively. Combined overwinter predation rates of collared mule deer ranged from an apparent low estimate of 0.09 during the winter of 2013-2014 to a high of 0.33 during the winter of 2010-2011; median overwinter predation rate across the six years was 0.13 (Table 1.1). Of the predation events where a predator was identified, coyotes preyed on significantly more mule deer than the other predators, primarily targeting fawns (CIF = 5.05, p = 0.02, all other p values > 0.50). Cumulative predation rates across all years were 0.05 for coyote predation, 0.02 for cougar predation, 0.01 for bobcat predation, 0.002 for bear predation, and 0.09 for unknown predation (Table 1.1). The proportions of fawn predation by cause were 0.47 unknown, 0.31 coyote, 0.11 cougar, 0.10 bobcat, and 0.01 bear. Adult female mule deer predation by cause were 0.58 unknown, 0.19 cougar, 0.18 coyote, 0.3 bobcat, and 0.2 bear.

Predator-specific predation risk

Canid predation events were randomly distributed relative to environmental characteristics measured; terrain ruggedness, snow depth, habitat type, and distance to ecotone edge (Table 1.2). Conversely, RSF and LSDF models indicated felid predation of mule deer occurred preferentially in deeper snow relative to availability across the landscape ($\beta = 0.24$) and to prey

distribution (β = 0.19; Table 1.2; Figure 1.2). Felid predation events were more strongly influenced by anthropogenic features compared to canid predations; felid predation locations were further from pipelines relative to availability across the landscape (β = 0.35) and to prey distribution (β = 0.72), and were closer to primary (β = -0.29) and secondary (β = -0.19) roads than expected relative to mule deer distributions (Table 1.2; Figure 1.2). RSF models indicated that canids and felids killed further from producing well pads than expected relative to availability across the landscape (β = 0.21, β = 0.27), while LSDF models indicated that only canids killed further from well pads relative to prey distributions (β = 0.23). RSF and LSDF models also indicated that canids preyed on mule deer closer to drilling wells (β = -0.12, β = -0.26, respectively; Table 1.2), however the median predation distance to a drilling well pad was 4.9 km, suggesting this result may not be biologically relevant (SE = 1028.13 m; Appendix 1.1).

Predation during high development activity

During the period of high energy development (2008-2011), RSF models indicated that predation sites occurred further from producing well pads than expected based on availability in the developed area (β = 0.24; Table 1.3, Appendix 1.1). Predation sites occurred in proportion to availability for all other anthropogenic features regardless of level of development. RSF models also indicated that predation locations occurred more often than expected in areas of shrub cover in the undeveloped area (β = 0.62) and in deeper snow in the developed area (β = 0.12; Table 1.3; Figure 1.3). Terrain ruggedness and distance to ecotone edge between trees and shrubs were not strong predictors of predation site locations.

Relative to mule deer distributions, LSDF models indicated predation sites occurred further from pipelines in both the undeveloped (β = 0.74) and developed (β = 0.19) areas, and closer to primary roads only in the undeveloped area (β = - 0.27). Distance to pipelines had the

greatest influence of all the measured variables during the high activity period (Table 1.3, Appendix 1.1). With respect to natural landscape features, locations of predation sites were similar to those assessed with the RSF. In the undeveloped and developed area, predation sites occurred more than expected based on mule deer distribution in areas of increased shrub cover relative to tree cover (β = 0.57 undeveloped, β = 0.30 developed) and in deeper snow in both areas (β = 0.19, β = 0.20, Table 1.3).

Predation during low development activity

During the period of low energy development (2012-2014), RSF models for the undeveloped and developed areas indicated that predation locations occurred closer to drilling well pads (β = -1.4 undeveloped, β = -0.16 developed) and further from producing well pads (β = 0.84, β = 0.24) than expected relative to the availability of that feature (Table 1.3, Appendix 1.1). Predation sites occurred in proportion to the availability of pipelines and roads. With respect to natural landscape variables, predation sites occurred more than expected in trees than shrubs in the undeveloped area (β = -0.49), whereas predation sites occurred in areas of less tree cover in the developed area (β = 0.48, Table 1.3). Neither terrain ruggedness, snow depth, nor distance to ecotone edge were strong predictors of predation sites in the low activity period.

LSDF models for the undeveloped and developed areas indicated predation locations occurred closer to drilling well pads (β = -0.51 undeveloped, β = -0.30 developed), further from producing well pads (β = 0.55, β = 0.24), further from pipelines (β = 0.32, β = 0.40), and closer to primary roads (β = --0.31, β = -0.33) relative to the distribution of mule deer (Table 1.3, Figure 1.3, Appendix 1.1). Additionally, in the developed area, predation sites also occurred closer to secondary roads (β = -0.22) and industrial facilities (β = -0.11, Table 1.3), but predation sites were further from industrial facilities that bordered the undeveloped area (β = 0.51, Table

1.3, Appendix 1.1). Predation sites were more likely to occur in non-forested habitats than expected based on mule deer distribution in both the undeveloped ($\beta = 1.01$) and developed ($\beta = 0.56$) areas (Table 1.3). As with the RSF results, terrain ruggedness, snow depth and distance to ecotone edge were not strong predictors of predation sites.

DISCUSSION

Human-caused habitat change is the primary disturbance influencing carnivore populations globally (Crooks et al. 2011; Ripple et al. 2014), with subsequent effects on interactions with prey species (Estes et al. 2011). While the impacts of this anthropogenic stressor on wildlife behavior has been well documented, interspecific interactions are a critical, but underserved area for investigation (Northrup and Wittemyer 2013). We recorded coyote, cougar, bobcat, and black bear predation on ≥ 6 month old mule deer in our study area, all of which are documented predators of mule deer in the intermountain West (Unsworth et al. 1999), though black bears were hibernating during most of the study period examined. Coyotes were the primary documented predator of wintering deer within our sample, accounting for over half of the identified predation events, while cougars constituted the majority of the remaining identifiable predations at slightly under one third of the events. Coyotes were the predominant identified predator of fawns, and cougars were the primary identified predator of adult females, consistent with prior studies (Unsoworth et al. 1999; Bishop et al. 2005; Hurley et al. 2011). Predation is most often the major proximate cause of mule deer mortality and generally considered compensatory (Bartmann et al. 1992; Bishop et al. 2005). In our study, we did not assess the impact of predation on mule deer population trends, though it is notable that the population

increased during the study and that survival of adult females and fawns > 6 months was similar between study areas (Northrup et al. *in revision*).

Predicting and describing patterns of predation is difficult, and is further complicated in ecosystems with varying levels of anthropogenic disturbance over wide spatiotemporal extents. Our approach allowed us to examine how anthropogenic disturbance and natural landscape features structure spatial patterns of 'true' predation risk (i.e., the probability of mortality by predation; Moll et al. 2017), while accounting for prey distribution. Predator hunting strategies also influence predation risk, with felid predators that commonly exhibit a sit and pursue ambush strategy evoking stronger risk effects than active, or cursorial, predators such as canids (Preisser et al. 2007). Accordingly, we also observed stronger relationships between felid kill sites and landscape structure than among canid kill sites, ultimately influencing many of the detected spatial patterns in predation risk to mule deer. By employing resource selection functions (RSF) and latent selection difference functions (LSDF), we were able to interpret the different roles of the spatial arrangements of landscape features *and* the distribution of mule deer on predation risk. Had we considered only habitat characteristics and not accounted for prey distribution, we would not have been able to evaluate adequately the factors contributing to spatial predation risk (Moll et al. 2017).

Anthropogenic effects on predation

Linear features (i.e., pipelines and roads) had the most consistent effect on predation site locations in this study, though in a complex manner. LSDF analyses demonstrated that, relative to deer distribution, predation sites occurred further from pipelines in all study sites and periods and closer to primary roads except for when human disturbance was highest. Conversely, RSFs indicated predation took place in proportion to the availability of these features across the

landscape. These patterns appeared predominantly to reflect felid predation, which was closer to roads and further from pipelines compared to kills by coyotes.

Linear corridors can alter movement patterns and species interactions depending on whether the feature is perceived as a travel corridor or barrier (Brittingham et al. 2014). When humans are not immediately present, carnivores may increase their use of human infrastructure as travel routes (Kertson et al. 2011; Knopff et al. 2014), which can increase predation risk for prey near these features (Whittington et al. 2011). Mule deer in the Piceance Basin have been observed to select for habitats closer to roads at night (Northrup et al. 2015). The combined effects of selection by prey for areas closer to roads, restricted movement or escape abilities which has been observed in other systems (Dyer et al. 2002), and the use of roads with low human activity by carnivores, could account for the observed increased predation risk near roads. While an interaction between snow and pipelines reduced the benefit of pipelines as travel corridors to coursing predators in the boreal forests of Canada (Dickie et al. 2017), pipelines inhibited predation in the Piceance irrespective of snow depth. Other aspects of pipelines may be reducing predation risk in our system, for example increased visibility of predators by mule deer.

Results from the RSF and LSDF analyses consistently indicated that predation sites occurred further from producing wells in the developed site regardless of activity level. Producing well pads were the only anthropogenic landscape feature avoided in predation site selection relative to both habitat availability and mule deer distribution. These combined results suggest producing well pads may serve as a predatory shield (Berger 2007) and might explain the documented selection for areas close to producing well pads by deer in this area (Northrup et al. 2015). The closest distance a predation site occurred to the edge of a producing well pad was ~140 m during the period of high activity and ~70 m during the period of low activity, while

mule deer locations occurred directly on the well pads in both periods. Well pads are relatively large swaths of land (average well pad = 3.4 ha) that have been cleared of vegetation, reducing concealment cover for predators to ambush attack prey, and, in turn, providing prey with increased detection abilities.

Predation events were closer to industrial facilities and drilling pads than expected based on mule deer distributions during the low activity period. However, the median distance of kill sites and mule deer locations were greater than 4 km from drilling pads and 1.5 km from industrial facilities, distances that are unlikely to have biological meaning given the topographic diversity of the study area. Thus, we do not think much can be gleaned from these results.

Effects of natural landscape features on predation

We observed a strong response to snow depth in the high activity period and vegetation cover across both periods, indicating these natural landscape features enhanced predation risk. It is well established that snow depth influences the locomotion of ungulates (Telfer and Kelsall 1984; Parker et al. 1984) and carnivores (Crête and Larivière 2003; Murray and Boutin 1991). The effect of snow, in turn, influences predation risk (Husseman et al. 2003; Telfer and Kelsall 1984), with the advantage often given to predator, which have lower foot-loads (ratio of body mass to foot area) than their ungulate prey. This appeared to be particularly the case for felid predators. Accordingly, mule deer were more likely to be preyed upon in deeper snow relative to their use in both study sites, and in deeper snow relative to availability in the developed site. Cumulative snowfall was lower during the period of low relative to high activity when averaged across years, though the winter of 2010-11 had the greatest yearly snowfall. We speculate that, on average, snow was below a depth that influences deer locomotion (Parker et al. 1984) which may, in part, explain why snow depth was less influential during the low activity period.

Cougars will often kill prey in steeper terrain with greater cover while coyotes prefer more open habitat (Bishop et al. 2005), though not always (Elbroch et al. 2013). Contrary to expectations, we did not detect a strong influence of terrain ruggedness on predation site locations. We also did not observe a response in predation site selection to ecotone edge between forested and shrub habitats, which has been observed to facilitate effective predation in similar systems (Laundré and Loxterman 2007; Elbroch et al. 2013). The highly fragmented landscape of the Piceance Basin may provide so much edge habitat that any selection may not be observable. In the Piceance Basin, mule deer select shrub habitats over trees, particularly during the night (Lendrum et al. 2012; Northrup et al. 2015), and predation was found to occur in shrub lands more than treed areas. In combination with greater deer availability, dense shrub stands may provide greater concealment cover for predators than the relatively open understory of the pinyon-juniper woodland. The removal and disturbance of sagebrush habitat for expansion of energy infrastructure (Brittingham et al. 2014) has the potential to limit hunting habitat for carnivores.

Conclusions

Animals alter their behavior in association with natural and anthropogenic habitat alterations through the spatial selection or avoidance of an area (Laberee et al. 2014), which influences interspecific interactions. We observed that landscape features associated with energy development altered predation risk in this system. Specifically, we note that some features (pipelines and well pads) appeared to inhibit predation, while others (namely roads) were affiliated with predation, making a simplified assessment of the impact of development on predator-prey dynamics difficult. In areas where predation of mule deer is a concern, a reduction in road development may merit consideration by managers.

In predator-prey interactions, the benefit to one guild is often a detriment to the other and therefore must be considered when making informed management decisions, especially during a time of unprecedented human-induced landscape alteration. Disentangling the intricacies of interspecific interactions in landscapes altered by human activities is challenging and it is even more difficult to relate these metrics to demographic effects. When data are available, combining resource selection functions and latent selection difference functions resolves some of the spatial complexity and can serve as a template to further our understanding of predation risk in anthropogenically altered landscapes.

Table 1.1. Annual numbers of radio-tracked mule deer, cumulative predation rate, number of mule deer preyed upon by each predator (including unknown), cumulative precipitation (cm), average temperature, and the number of well pads in the development phase, during the winter in the Piceance Basin, CO, USA, 2008-2014.

Year	Collared deer *	Cumulative predation Rate	Cause of predation					Cumulative precipitation (cm)	Temp (C)	Drilling well pads
			Coyote	Cougar	Bobcat	Bear	Unknown			
08-09	187	0.13	8	2	5	0	10	15.53	0.00	30
09-10	250	0.11	9	2	5	0	11	14.25	-0.24	24
10-11	267	0.33	24	14	8	1	41	21.52	-0.64	11
11-12	295	0.25	21	9	3	2	39	13.04	1.80	3
12-13	316	0.14	15	6	2	0	20	12.92	-1.56	3
13-14	307	0.09	3	4	1	1	20	19.96	1.00	1

* Includes recaptures from the previous year so totals do not equate to the total number of individuals collared.

Table 1.2. Median standardized parameter estimates of predation sites of radio-collared mule deer by canid (coyote) and felid (cougar and bobcat) predators from resource selection functions (RSF) and latent selection difference functions (LSDF) during the winter in the Piceance Basin, CO, USA, 2008-2014.

	Canid		Felid	
Covariate	RSF	LSDF	RSF	LSDF
Ruggedness	-0.208	-0.185	0.809	0.795
Snow depth	0.068	0.091	0.235*	0.191*
Open habitat	0.355	0.418	-0.355	-0.309
Shrub habitat	0.351	0.310	-0.022	0.078
Distance to				
Habitat edge	0.044	-0.010	-0.015	-0.018
Drilling wells	-0.117*	-0.257*	-0.084	-0.132
Producing wells	0.207*	0.233*	0.265*	0.188
Pipelines	-0.150	0.046	0.353*	0.722*
Primary roads	0.123	-0.080	-0.031	-0.292*
Secondary roads	0.051	0.004	-0.148	-0.188*
Facilities	0.060	-0.020	0.450*	0.225

* Indicates ≥ 90% of the posterior distributions for the standardized β coefficients did not overlap zero

Table 1.3. Median standardized parameter estimates of predation sites of radio-collared mule deer from resource selection functions (RSF) and latent selection difference functions (LSDF) in periods of high and low energy development in undeveloped and developed study areas during the winter in the Piceance Basin, CO, USA, 2008-2014.

	High activity				Low activity			
	Undeveloped		Developed		Undeveloped		Developed	
Covariate	RSF	LSDF	RSF	LSDF	RSF	LSDF	RSF	LSDF
Ruggedness	0.57	0.33	0.68	0.47	0.02	-0.06	-0.68	-0.75
Snow depth	0.13	0.19*	0.12*	0.20*	0.07	0.03	0.09	0.10
Open habitat	-0.14	0.14	-0.13	-0.25	0.54	1.01*	0.48*	0.56*
Shrub habitat	0.62*	0.57*	0.25	0.30*	-0.49*	-0.45	0.20	0.40*
Distance to								
Habitat edge	-0.16	-0.17	0.09	0.11	-0.05	-0.04	0.02	0.00
Drilling wells	-0.05	-0.02	0.03	0.12	-1.4*	-0.51*	-0.16*	-0.3*
Producing wells	0.14	-0.08	0.24*	0.23*	0.84*	0.55*	0.24*	0.24*
Pipelines	0.21	0.74*	0.01	0.19*	0.07	0.32*	0.10	0.40*
Primary roads	0.01	-0.27*	0.03	-0.06	-0.08	-0.31*	0.03	-0.33*
Secondary roads	-0.13	-0.13	0.07	0.07	0.12	0.10	-0.12	-0.22*
Facilities	0.14	-0.03	0.01	0.00	0.30	0.51*	-0.06	-0.11*

* Indicates ≥ 90% of the posterior distributions for the standardized β coefficients did not overlap zero

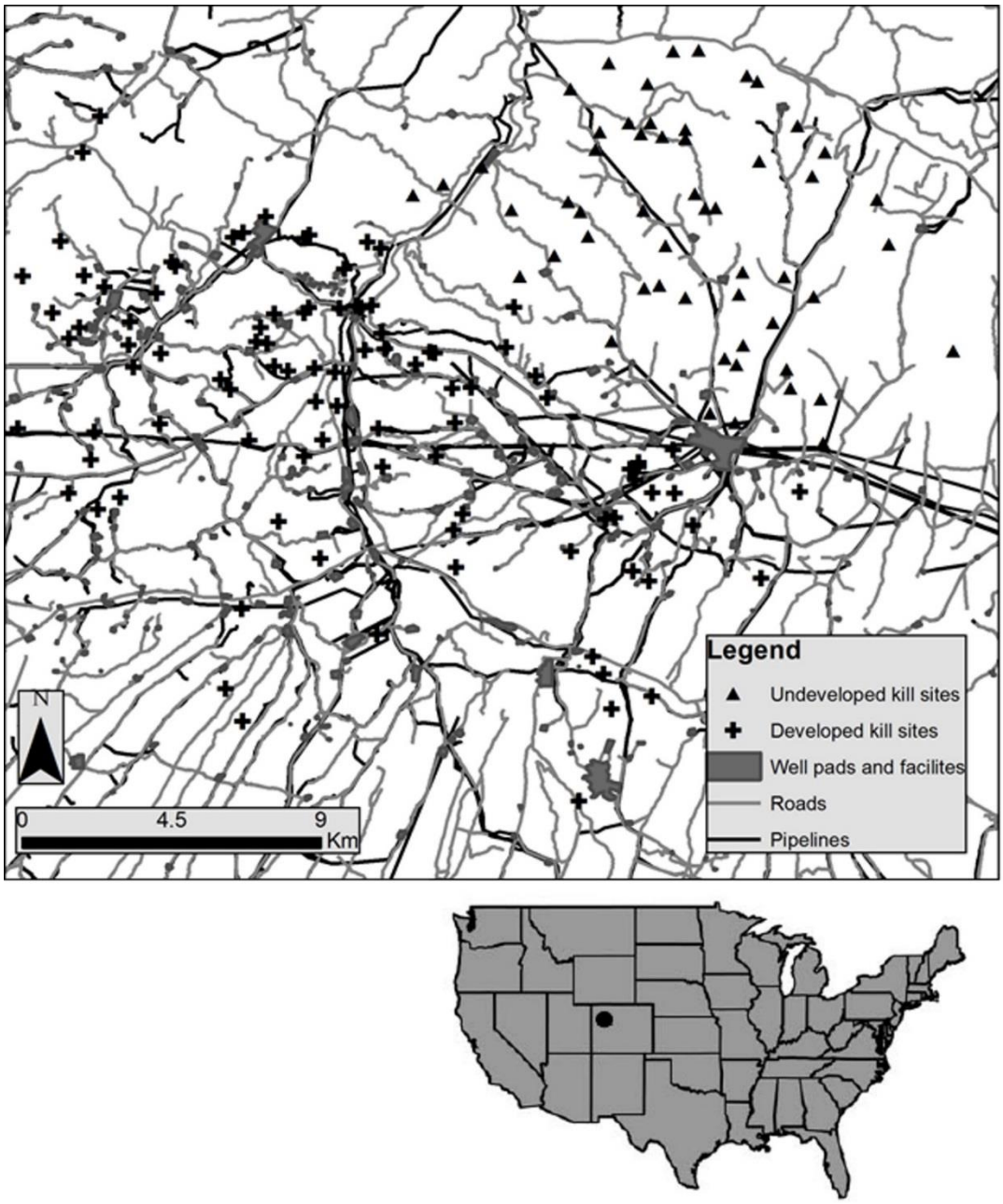

Figure 1.1. Locations of mule deer predation sites and natural-gas development infrastructure in the Piceance Basin, CO, USA during the period of high development, 2008-2011, across undeveloped and developed study sites.

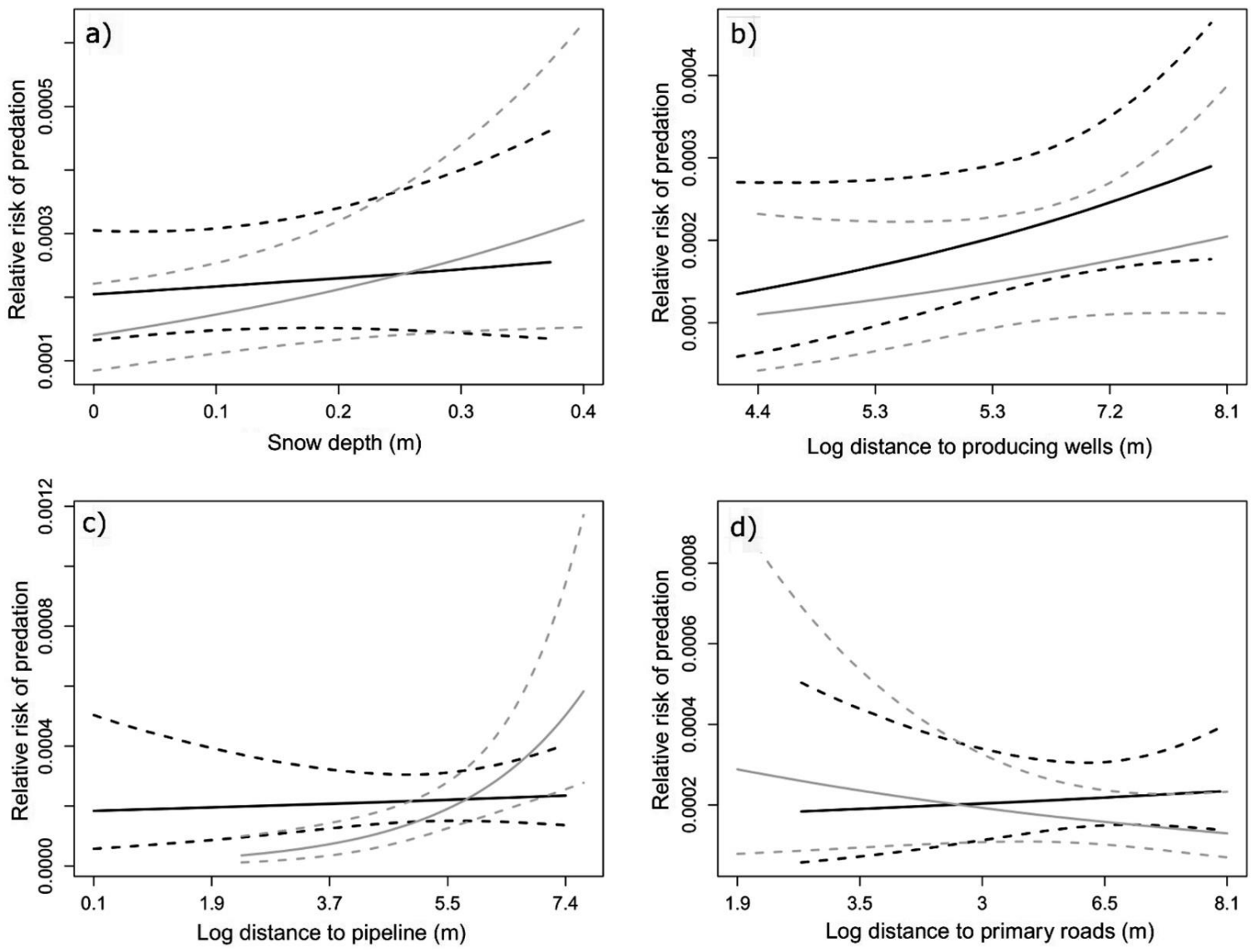
a)
Relative risk of predation
0.0001
0.0003
0.0005
0
0.1
0.2
0.3
0.4
Snow depth (m)
b)
Relative risk of predation
0.0001
0.0002
0.0003
0.0004
4.4
5.3
5.3
7.2
8.1
Log distance to producing wells (m)
c)
Relative risk of predation
0.0000
0.0004
0.0008
0.0012
0.1
1.9
3.7
5.5
7.4
Log distance to pipeline (m)
d)
Relative risk of predation
0.0002
0.0004
0.0006
0.0008
1.9
3.5
3
6.5
8.1
Log distance to primary roads (m)

Figure 1.2. Median standardized parameter estimates (solid lines) and 95% credible intervals (dashed lines) of predation sites of radio-collared mule by canids (black) and felids (grey) in the Piceance Basin, CO, USA: a) RSF output indicates the relative risk of predation by felids increased in deeper snow than expected based on habitat availability b) LSDF output indicates the relative risk of predation increased by canids and felids further from well pads than expected based on mule deer distribution; c) LSDF output indicates the relative risk of predation by felids increased further from pipelines than expected based on deer distribution; d) LSDF output indicates the relative risk of predation by felids increased closer to primary roads than expected based on mule deer distribution.

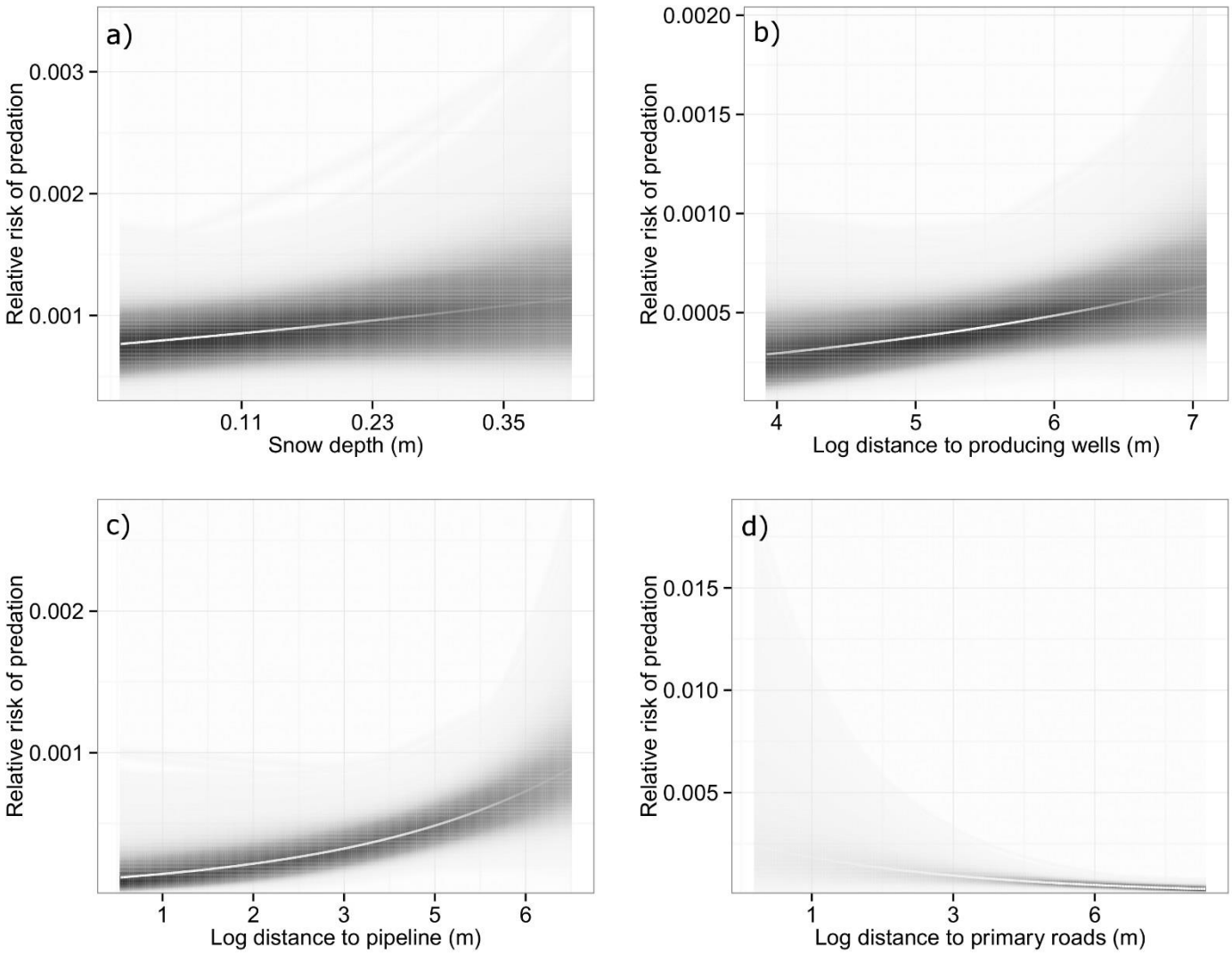
a)
Relative risk of predation
0.003
0.002
0.001
0.11
0.23
0.35
Snow depth (m)
b)
Relative risk of predation
0.0020
0.0015
0.0010
0.0005
4
5
6
7
Log distance to producing wells (m)
c)
Relative risk of predation
0.002
0.001
1
2
3
5
6
Log distance to pipeline (m)
d)
Relative risk of predation
0.015
0.010
0.005
1
3
6
Log distance to primary roads (m)

Figure 1.3. Posterior distribution of predicted mule deer predation site selection in the Piceance Basin, CO, USA: a) RSF output indicates the relative risk of predation increased in deeper snow than expected based on habitat availability in the developed area during the period of high activity; b) LSDF output indicates the relative risk of predation increased further from well pads than expected based on mule deer distribution; c) LSDF output indicates the relative risk of predation increased further from pipelines than expected based on deer distribution; d) LSDF output indicates the relative risk of predation increased closer to primary roads than expected based on mule deer distribution.

CHAPTER TWO

CHANGES IN CIRCADIAN ACTIVITY PATTERNS OF A WILDLIFE COMMUNITY POST HIGH-INTENSITY ENERGY DEVELOPMENT

INTRODUCTION

Human-induced environmental change is occurring at unprecedented rates and threatens wildlife worldwide (Pimm and Raven 2000). Over time, organisms can adapt to altered environmental conditions that impose selective pressures; however, because anthropogenic landscape change occurs over relatively short time scales, organisms may not be able to adapt rapidly enough, resulting in species declines and extinction (Sih et al. 2011; McDonnell and Hahas 2015). Behavioral plasticity, through which animals react differently to various stimuli, can play an important role in an organism's ability to survive in novel landscapes (Wong and Candolin 2015). Understanding the ability of animals to behaviorally adjust to human disturbance can provide critical information on their risk status that can inform conservation and management activities (Caro 2007; Barrueto et al. 2014).

One mechanism through which anthropogenic disturbance can influence ecological processes is by altering the temporal distribution of species (Wong and Candolin 2015). Wildlife vary activity to match and adjust to environmental conditions, interference from competitors, predation risk, forage or prey availability, and life-history characteristics in ways that maximize fitness. As such, predators are expected to optimize their hunting efficiency by exploiting periods of prey vulnerability while minimizing competition with other predators, and prey species must balance optimal feeding opportunities with competition and predation risk (Ross et al. 2013).

These interactions can be altered by the perceived or real threat resulting from anthropogenic disturbance (Vistnes and Nellemann 2008; Barrueto 2014). Alterations to activity patterns can affect physiology (Creel et al. 2002; Millspaugh et al. 2001), human-wildlife conflict (Woodroffe et al. 2005), and interspecific interactions (Hebblewhite et al. 2005; Barrueto et al. 2014).

Habitat loss has been identified as affecting 40 percent of the world's mammals (Schipper et al. 2008). The combined effects of exurban sprawl and energy development are the largest drivers of land use change in western North America (Naugle and Copeland 2012), with energy development alone expected to disturb over 200,000 km^2 of new area in the coming decades (McDonald et al 2009). The Piceance Basin in northwestern Colorado, USA, contains one of the largest natural gas reserves in the country (Sawyer et al. 2009) and experienced rapid landscape change in the form of energy infrastructure development from 2000-2011 (Colorado Oil and Gas Commission; http://cogcc.state.co.us/data2.html#/downloads). Since 2012, the Piceance Basin has primarily been in a state of natural gas extraction and production rather than development. These different stages of hydrocarbon extraction are accompanied by pronounced differences in human activity, with higher levels of human activity when well pads are actively being drilled (Sawyer et al. 2009). While previous studies have demonstrated the impacts of energy extraction during the high-intensity development phase (Laberee et al. 2004; Sawyer et al. 2006; Lendrum et al. 2012), responses detected during the high-intensity phase may not be representative of longer-term responses. Changes in animal behavior in response to disturbance may occur over short time periods, seconds to hours, but it can also persist from days to years (McDonnell and Hahas 2015); therefore, a better understanding of responses in animal behavior post high-intensity disturbances is warranted.

We tested whether the mammalian predator and prey community, including 2 carnivores (bobcats [*Lynx rufus*] and coyotes [*Canis latrans*]), 2 ungulates (mule deer [*Odocoileus hemionus*] and North American elk [*Cervus canadensis*]), and 2 broad groupings of small mammals (lagomorphs and rodents), displayed behavioral responses to energy development post development through shifts in temporal activity patterns. We assessed activity patterns among 3 diel periods (crepuscular, day, and night) using motion-triggered digital cameras placed across 2 contiguous areas of the Piceance Basin that experienced markedly different levels of development: a relatively undisturbed site and a highly disturbed site. Because animals may alter their behavior in association with natural and anthropogenic habitat alterations through temporal shifts (Laberee et al. 2014), we tested the hypothesis that large mammals (carnivores and ungulates) would exhibit different temporal activity patterns between the developed and undeveloped sites whereas the smaller mammals (lagomorphs and rodents) would not. Carnivores (bobcats and coyotes, Tigas et al. 2002) and ungulates (elk, Naylor et al. 2009; mule deer, Northup et al. 2015) will display behaviorally driven avoidance of human activities and habitat fragmentation; therefore, we predicted that bobcats, coyotes, mule deer, and elk in the developed site would be less active during the day when the perceived threat of humans would be highest (Frid and Dill 2002), compared to the undeveloped site.

METHODS

Study area

We monitored activity patterns of the wildlife community by placing cameras across ~ 162 km^2 in the Piceance Basin of northwest Colorado, USA (39.924586° N, -108.197458° W). The Piceance Basin, a designated critical winter range habitat, is home to one of the largest migratory

mule deer herds in the U.S., and the second largest natural gas reserve in the U.S. (Hawkins et al. 2016). Within the basin, levels of natural gas extraction vary markedly. We examined these differences by recording data in 2 subsections of the study area: an undeveloped area (79 km^2, 0.1 well pads and facilities/km^2) and a developed area (83 km^2, 0.8 well pads and facilities/km^2; Figure 2.1). The 2 areas are contiguous with consistent habitat and topography, but distinct in relation to levels of development and that they are inhabited by 2 subpopulations of mule deer that display different migratory behaviors (Lendrum et al. 2012).

The study area ranged in elevation from ~1,800 to 2,285 m, and was characterized by cold winters with most precipitation occurring as snowfall. Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) were the dominant overstory species; common shrubs included big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentate*), Gamble's oak (*Quercus gambelii*), mountain snowberry (*Symphoricarpos oreophilus*), and rabbitbrush (*Crysothamnus* spp.; Lendrum et al. 2014). Common species of large mammals included coyotes, bobcats, mule deer, and elk, while cougars (*Puma concolor*) and black bears (*Ursus americanus*) occurred with less frequency. Smaller mammals included mountain cottontails (*Sylvilagus nuttallii*.), an occasional black-tailed jackrabbit (*Lepus* spp.), and various rodent species of which golden-mantled ground squirrels (*Callospermophilus lateralis*) and chipmunks (*Tamias sp.*) were most common.

Data collection

To quantify animal activity, we obtained data from 40 passive infrared Reconyx PC 800 digital cameras (Reconyx, Holmen, Wisconsin) from 2015-2016 across the study area, with 20 cameras in each subsection (Figure 2.1). To provide adequate coverage, cameras were deployed in a

systematically random design with each camera being randomly placed within a 2 x 2 km grid across the entire study area while maintaining a minimum distance of ≥ 500 m between cameras in neighboring cells (Alonso et al. 2015; Lewis et al. 2015). Cameras were placed as close as possible to each randomly chosen camera station, but near specific features expected to maximize capture probability, such as dirt roads, wildlife trails, and water sources. Stations consisted of a single digital camera trap unit set on a tree or post at a height of approximately 40 cm, facing perpendicular to the expected direction of animal travel and approximately 3 m from the anticipated site of capture. All cameras were programed to include a date and time stamp to each photograph making the monitoring of activity patterns feasible. Photographs were catalogued using the Colorado Parks and Wildlife photo database (Newkirk 2014). Only photographs collected from 1 October 2015 through 31 March 2016 were included in the analyses to best ensure a closed system based on mule deer migration patterns in the region (Lendrum et al. 2013, 2014). Because we were interested in comparing activity patterns between levels of development and not in characterizing general activity patterns, one complete season provided the necessary data.

For each camera location, environmental characteristics including elevation, slope, and aspect were derived from a digital-elevation model (DEM) at a resolution of 30 m (http://datagateway.nrcs.usda.gov/) using ArcGIS 10.2.2 (Esri, Redlands, California). Similarly, habitat type was characterized using the U.S. Department of Agriculture National Land Cover Dataset, and simplified into either a shrub or tree designation (http://datagateway.nrcs.usda.gov/).

Data analyses

We categorized the proportion of each 24-hour day as crepuscular (representing the civil dawn or twilight when light is visible but the sun is not), day (sunrise to sunset), or night (when no light from the sun is visible) to calculate the 'expected proportion' of samples for each target species assuming uniform activity over a 24-hr day. We determined these 3 categories on the 15th day of each month and assigned those hours to the entire month. Therefore, the expected percent of available hours averaged across the 6 winter months included: crepuscular, 12.5%; day, 47.7%; and night, 45.8%.

For each study area (undeveloped and developed), we binned all photographs into the corresponding temporal category and counted the number of independent photographs of our 6 target species: bobcats, coyotes, mule deer, elk, lagomorphs, and rodents. We considered photographs taken at the same camera site of the same species to be independent if images were obtained ≥ 1 hr apart (Lewis et al. 2015). The total number of independent photographs for each temporal category was then divided by the number of hours available in the corresponding category (crepuscular, day, night) to provide an 'observed proportion' of detections attributable to each diel period.

Statistical methods

We used Fisher's exact test to examine if there was a difference in categorical habitat type (shrub or tree) at camera locations between study areas, and 2-sample *t*-tests (Zar 1999; $\alpha = 0.05$) to compare differences in continuous variables (elevation, slope, and aspect) across sites. All statistical analyses were performed in R v 3.3.1. Chi-square goodness-of-fit tests were used to test whether the observed proportions of photographs for the 3 temporal periods in the undeveloped and developed study areas differed from the expected proportions of available

hours in each period. Additional Chi-square goodness-of-fit tests also were performed to compare the developed site to the undeveloped site using the same approach.

To provide an ecological interpretation for comparisons that were deemed statistically different, the difference in proportions of activity was calculated as odds ratios for each pairing (i.e., bobcat photographs in the developed and undeveloped site during crepuscular hours; Rita and Komonen 2008). We first transformed the proportion (p) of photographs obtained for each category into odds, defined as $p/(1-p)$, the ratio of the probability that an incident takes place to the probability that it does not. We then compared the 2 proportions by using their ratios: odds ratio = odds(p_1)/odds(p_2) (Rita and Komonen 2008).

RESULTS

We deployed 40 cameras that operated for a total of 7,185 camera days, and obtained 5,675 photographs of our 6 target species. Of these, 3,067 met our criteria for independent detections. Lagomorphs and mule deer constituted the majority of photographs at 1,363 and 1,257, respectively (Table 2.1). Of the remaining 4 species, we captured 146 independent photographs of coyotes, 116 of rodents (primarily golden-mantled ground squirrels), 105 of elk, and 80 of bobcats. Environmental site characteristics were similar between camera placement in the undeveloped and developed study area for habitat type ($P = 0.48$), elevation ($t = 1.15$, $P = 0.26$), slope ($t = 0.84$, $P = 0.41$), and aspect ($t = 0.29$, $P = 0.77$).

Bobcats displayed activity patterns that differed from the proportion of available hours in the undeveloped ($\chi^2_2 = 9.12$, $P = 0.01$) and developed study sites ($\chi^2_2 = 29.12$, $P < 0.01$; Table 2.2). They were more active during crepuscular hours, less active during the day, and more active at night relative to availability (Table 2.2). Additionally, bobcats displayed different

activity patterns between the undeveloped and developed sites ($\chi^2_2 = 7.05$, $P = 0.03$; Table 2.2). Bobcats in the developed site were 2.94 times less active during the day, and 1.28 and 1.45 times more active during crepuscular and night times, respectively (Figure 2.2).

Coyotes also displayed activity patterns that differed from the proportion of available hours in the undeveloped site ($\chi^2_2 = 8.62$, $P = 0.01$), but not in the developed site ($\chi^2_2 = 2.68$, $P = 0.26$; Table 2.2). In the undeveloped site, coyotes were more active than expected during the crepuscular and day periods, and less active at night (Table 2.2). Similar to bobcats, activity patterns of coyotes varied between the undeveloped and developed study site as well ($\chi^2_2 = 13.79$, $P < 0.01$; Table 2.2). Coyotes in the developed site were 1.93 times less active during daylight hours, 1.92 times less active during crepuscular hours, and 2.98 times more active at night (Figure 2.2).

Similarly, mule deer also displayed activity patterns that differed from the proportion of available hours in the undeveloped site ($\chi^2_2 = 10.56$, $P < 0.01$), but not in the developed site ($\chi^2_2 = 0.55$, $P = 0.76$; Table 2.2). The most pronounced differences in the undeveloped site were increased activity during the day and decreased activity during the night relative to availability (Table 2.2). Activity patterns also differed between the undeveloped and developed site ($\chi^2_2 = 7.73$, $P = 0.02$; Table 2.2). Mule deer were 2.10 times less active during the day and 2.21 times more active at night in the developed than undeveloped site (Figure 2.2).

As observed with coyotes and mule deer, elk also displayed activity patterns that differed from the proportion of available hours in the undeveloped site ($\chi^2_2 = 7.46$, $P = 0.02$), but not in the developed site ($\chi^2_2 = 2.91$, $P = 0.23$; Table 2.2). In the undeveloped site, elk were more active during crepuscular hours and less active during the night (Table 2.2). Elk activity patterns did not

consistently differ between the undeveloped and developed sites and were characterized by erratic periods of activity ($\chi^2_2 = 2.60$, $P = 0.27$; Table 2.2; Figure 2.2).

Lagomorphs displayed activity patterns that differed from the proportion of available hours in the undeveloped ($\chi^2_2 = 17.1$, $P < 0.01$) and developed sites ($\chi^2_2 = 33.81$, $P < 0.01$; Table 2.2). Similar to bobcats, they were more active during crepuscular hours, less active during the day, and more active at night relative to availability (Table 2.2). Lagomorphs did not appear to alter their activity patterns between the undeveloped and developed sites ($\chi^2_2 = 4.08$, $P = 0.13$; Table 2.2; Figure 2.2)

Rodents also displayed activity patterns that differed from the proportion of available hours in the undeveloped ($\chi^2_2 = 61.91$, $P < 0.01$) and developed sites ($\chi^2_2 = 34.90$, $P < 0.01$), but in the opposite pattern observed with lagomorphs (Table 2.2). They exhibited stronger diurnal activity, with > 80% of photographs occurring during the day, and were less active at night and during crepuscular hours than expected (Table 2.2). Even though the majority of activity occurred during the day, levels of activity still differed between the undeveloped and developed site ($\chi^2_2 = 7.32$, $P = 0.02$; Table 2.2). During the day, rodents were 2.85 times less active in the developed than undeveloped site (Figure 2.2).

DISCUSSION

Animals respond to human-induced environmental change in different ways depending on their behavioral plasticity and life-history characteristics (Sih et al. 2011; Wong and Candolin 2015). Human-mediated landscape change, a dominant driver of impacts on wildlife, can induce immediate and long-term alterations to animal behavior (McDonnell and Hahas 2015). We lack an understanding of the longitudinal effects of anthropogenic landscape change on wildlife

communities, particularly in areas where levels of human activity decline over time. Avoidance behavior by mammals is plastic and can revert to pre-disturbance behavior once the disturbance has declined or dissipated (Kitchen et al. 2000; reviewed in Lowry et al. 2013). In this study, we observed behavioral differences in all components of the mammalian community that we examined that indicated animals are responding to energy extraction 5 years after high-intensity development had ceased and transitioned into the production phase. Bobcats, coyotes, and mule deer were less active during the day in the area of high well pad density compared to the undeveloped site, as were rodents, which was unexpected. Aside from the markedly different levels of energy development, other environmental variables measured were similar between sites, supporting our conclusion that the behavioral differences were related to anthropogenic disturbance to the landscape. The behavioral alterations we observed may be legacy effects from the initial intense energy development or may persist due to occasional vehicles or maintenance workers in the developed site, in a system that otherwise experiences little human disturbance.

Of the carnivore species examined, bobcats appeared to be most responsive to the perceived human disturbance during the day. Although bobcats were largely crepuscular and nocturnal, possibly in response to the nocturnal activity patterns of their primary prey, lagomorphs, they were nearly 3 times less active during the day in the developed site than the undeveloped site. Similarly, Tigas et al. (2002) observed reduced daytime activity of radio-collared bobcats in areas of increased habitat fragmentation compared to unfragmented habitat. Previous research also has observed the probability of detecting bobcats at camera stations decreased with increasing human recreation, indicating they may reduce use of areas near human disturbance (George and Crooks 2006). While these previous studies demonstrated that bobcats

are sensitive to human activity, our research highlights that behavioral response to human-induced habitat alteration may persist even when humans are a minor presence on the landscape.

Coyotes are considered a generalist species, able to persist in a variety of habitats and subsist on a variety of food sources (Crooks 2002). Nevertheless, previous research has shown that coyotes also will alter their activity to minimize exposure at times when human disturbance is greatest (Kitchen et al. 2000; Tigas et al. 2002). This may reflect removal programs targeting coyotes across much of their range (Parker 1995). We observed that coyotes were approximately 2 times less active in the developed site during the day than in the undeveloped site, but unlike bobcats, coyotes appeared to compensate for their decreased diurnal activity by increasing their nocturnal activity by nearly 3 times. Our finding of greater plasticity in circadian activity in coyotes compared to bobcats is consistent with prior studies documenting less sensitivity to anthropogenic disturbance (e.g., urbanization) in coyotes relative to bobcats (Crooks 2002; Riley et al. 2003). Interestingly, Kitchen et al. (2000) noted that a coyote population was able to shift to increased diurnal activity 8 years after persecution had ceased. While we lack information on coyote activity during high-intensity development at our study site, daytime activity was less in the developed site than the undeveloped site 5 years post disturbance, indicating they have not yet returned to expected levels.

Predators can exert strong top-down pressures on their prey (Winnie and Creel 2016), therefore, we expected to see an increase in prey activity during the day in the developed site when bobcats and coyotes were less active, thereby reducing predation risk (Lima and Bednekoff 1999). This, however, was not the case. Lagomorphs did not alter their behavior between sites, whereas mule deer were less active during the day in the developed site compared to the undeveloped site. Within the ungulates, mule deer displayed more temporal variability in their

activity patterns than elk. However, elk were only photographed on 14 independent occasions in the developed site, limiting our interpretation of patterns. Mule deer were approximately 2 times less active during the day in the developed site and compensated for this by being 2 times more active at night in the developed site relative to the undeveloped site. This adjustment was similar to the pattern observed by coyotes, but we could not discern if the similarity is a response to human disturbance by both species, or a response by coyotes to match the activity of their winter prey.

Prior research has similarly found that mule deer altered their distribution in response to energy development, with greater displacement from human infrastructure during the day than at night (Northrup et al. 2015). Other studies have found variable responses to human recreationists by deer (George and Crooks 2006; Taylor and Knight 2003). As such, avoidance behavior of anthropogenic disturbance by mule deer may be site and condition specific. As observed in this study, large-scale habitat fragmentation in an area that receives little human recreation outside of the hunting season may be enough to alter mule deer behavior even when few humans are actually present.

Behavioral responses to human-induced environmental change varied across a wildlife community with some species being disproportionally affected, highlighting the variation in sensitivity among species and, potentially, their susceptibility to human disturbance (Crooks 2002). A better understanding of how multiple wildlife species within a community behaviorally respond to disturbances can inform species-specific management and conservation practices. For example, in this study system bobcats may best serve as a useful indicator species to anthropogenic disturbance because they appeared to be most affected by the landscape changes associated with energy extraction, even when human presence was minimal. This does not take

into account other anthropogenic disturbances that can alter the wildlife community in ways not examined by this study, such as increased hunting pressure associated with higher road densities (Trombulak and Frissell 2000), which must also be considered in multispecies conservation efforts. The integration of animal behavior into wildlife management can improve our efforts to manage and conserve wildlife in the face of continued anthropogenic disturbance.

Table 2.1. The number cameras that detected the 6 target species in each study site (20 cameras per site) and the number of independent photographs (separated by > 1 hour) that were captured in the Piceance Basin, northwestern Colorado, USA, October 2015 through March 2016.

	Cameras		Photographs	
	Undeveloped	Developed	Undeveloped	Developed
Bobcat	14	14	26	54
Coyote	16	18	74	72
Mule deer	19	20	557	700
Elk	13	8	91	14
Lagomorph	19	18	764	559
Rodent	9	7	83	33

Table 2.2. The percent of time each species was active during distinct diel periods (crepuscular, day, night) in the undeveloped and developed study site in the Piceance Basin, northwestern Colorado, USA, October 2015 through March 2016. The expected percent of available hours across diel periods as described in the text included: crepuscular, 12.5%; day, 47.7%; and night, 45.8%.

	Crepuscular		Day		Night	
	Undeveloped	Developed	Undeveloped	Developed	Undeveloped	Developed
Bobcat	23.08	27.78	23.08	9.26	53.85	62.96
Coyote	25.68	15.28	45.95	30.56	28.38	54.17
Mule deer	14.36	15.43	61.40	43.14	24.24	41.43
Elk	26.37	21.43	41.76	35.71	31.87	42.86
Lagomorph	19.37	19.53	15.31	6.51	65.31	73.96
Rodent	4.82	6.06	92.77	81.82	2.41	12.12

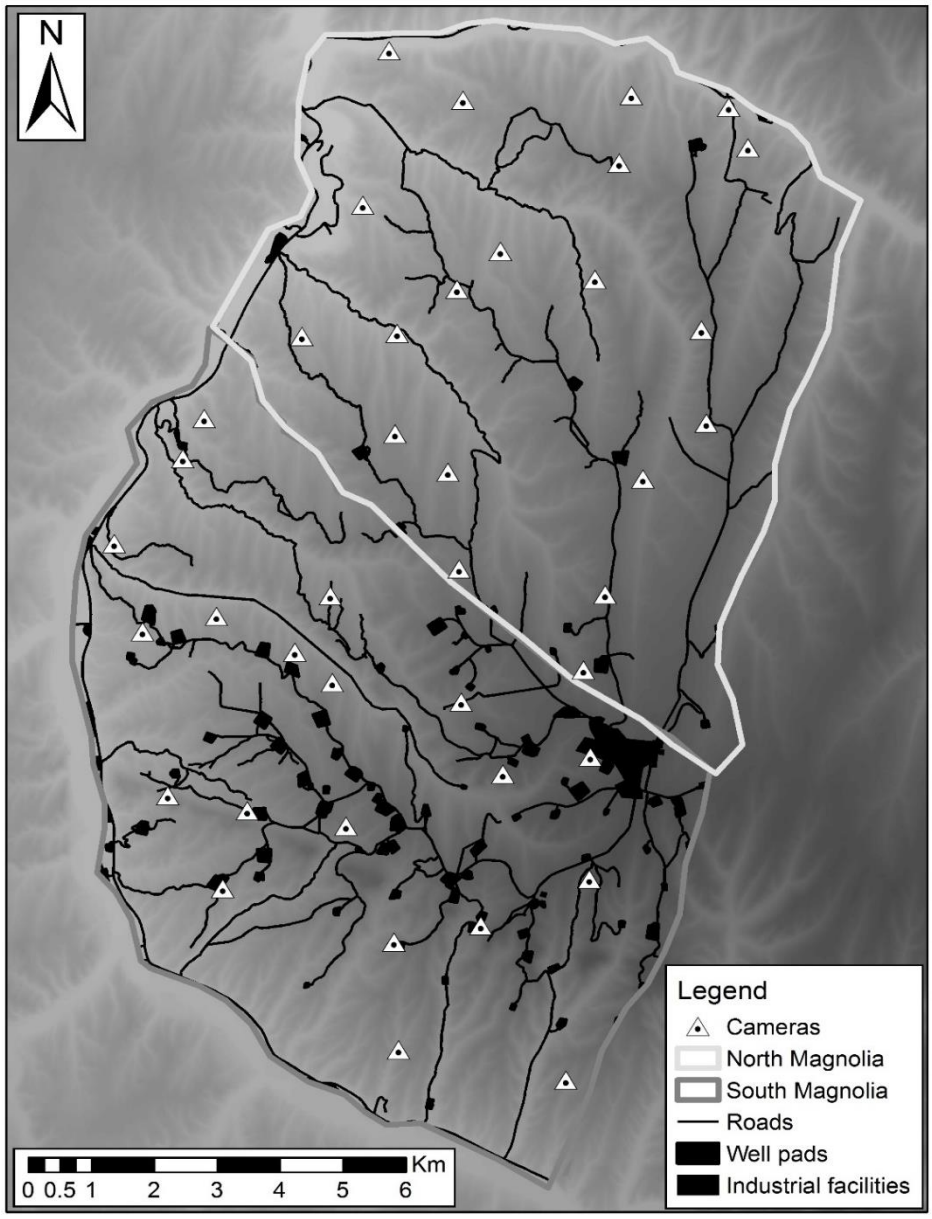

Figure 2.1. Undeveloped (North Magnolia) and developed (South Magnolia) study sites in the Piceance Basin, northwestern Colorado, USA, illustrating the distinct variation in levels of natural gas development and camera locations.

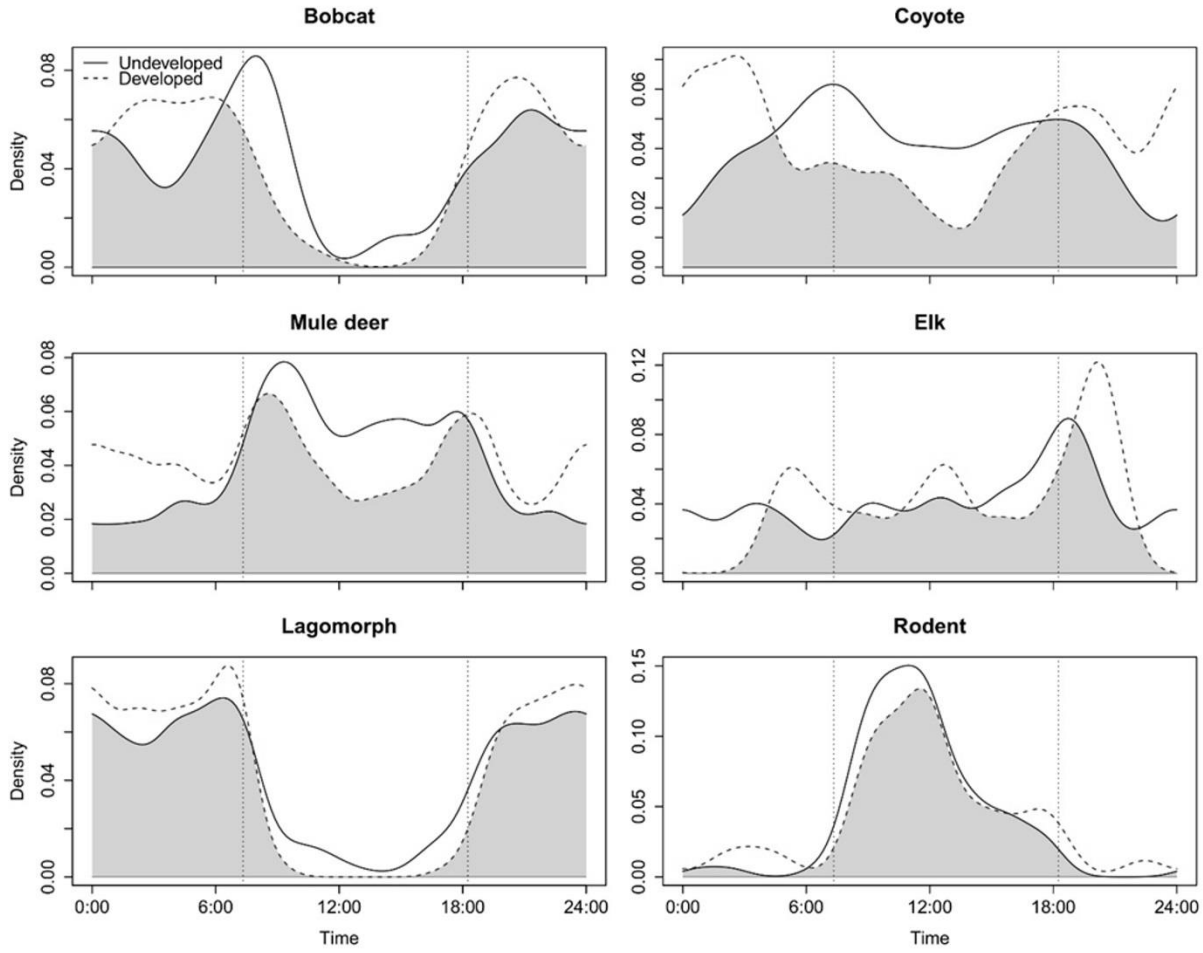

Figure 2.2. Temporal activity patterns of the 6 wildlife species in the undeveloped and developed study sites in the Piceance Basin, northwestern Colorado, USA, October 2015 through March 2016. Vertical dashed lines represent mean sunrise and sunset times during the 6 months of the study. Shaded sections indicate periods of temporal overlap.

CHAPTER THREE

RESIDUAL EFFECTS OF ENERGY DEVELOPMENT ON CARNIVORE COMMUNITY OCCURRENCE

INTRODUCTION

Wide-ranging species that occur at low densities and have a propensity for human-wildlife conflict, such as many mammalian carnivores, are thought to be particularly vulnerable to human-induced habitat alteration (Crooks 2002; Cardillo et al. 2004; Ripple et al. 2014). Globally, the majority of suitable carnivore habitat is influenced by anthropogenic disturbance (Crooks et al. 2017). Carnivores may avoid areas of elevated human activity (Wilmers et al. 2013; Lewis et al. 2015), a reduction in use that can persist even after human activity has largely ceased in a disturbed landscape (Lendrum et al. 2017a). Large carnivores also can have important roles in the structuring of ecological communities and provide economic services through ecotourism and sport hunting (Ripple et al. 2014). Consequently, their decline is of considerable conservation concern. As global infrastructure development rapidly converts natural habitat to human-dominated and fragmented landscapes, a better understanding of how carnivores respond to different types of development is warranted.

Energy extraction is rapidly expanding worldwide; the global demand for energy is projected to increase by 40% over the next 20 years (Northrup and Wittemyer 2013). Recent advances in technologies to extract hydrocarbon, such as hydraulic fracturing and horizontal drilling, have led to unprecedented rates of drilling (Kerr 2010), but can also be used to reduce the development footprint if applied in such an appropriate manner. From 2002 to 2012, ~3

million ha of central North America was occupied by well pads, roads, and storage facilities associated with oil and gas extraction (Allred et al. 2015). The infrastructure associated with energy development has been deemed a primary threat to wildlife (Kiesecker et al. 2009). Potential impacts to wildlife from oil and gas development include (1) behavioral alterations such as temporary displacement or range abandonment due to disturbances including vehicle traffic and noise associated with compressor stations, wells, and facilities, (2) direct loss of habitat from development, (3) habitat fragmentation from the pipelines, power lines, roads, and other facilities associated with development, (4) invasion of exotic plant species, and (5) direct mortality through increased human presence (Northrup and Wittemyer 2013). Furthermore, increased hunter access and harvest success resulting from energy development have direct conservation implications for wildlife management (Dorning et al. 2017).

Not all carnivores respond to anthropogenic disturbance similarly, however; certain species may exhibit greater tolerance to disturbance than others dependent on their life-history characteristics (Crooks 2002). In some cases, evidence of carnivore range expansions and population increases even appear to be on the rise despite the known detriments of anthropogenic disturbance (Larue et al. 2012), suggesting some species may be more adaptable and capable of using disturbed habitats than previously believed (Knopff et al. 2014). For example, roads may be avoided by animals when human activity is high, but selected for as suitable edge habitat or travel corridors when not in use (Knopff et al. 2014). However, high use of human-altered landscapes does not necessarily reflect quality habitat and may be attractive sinks or ecological traps that are maladaptive in the long term (Delibes et al. 2001). The behavioral responses by carnivores also can vary depending on the type and level of intensity of disturbances (Wilmers et al. 2013).

In order to accurately model species distributions, large numbers of observations are generally needed (Guisan and Zimmermann 2000); however, the behavioral traits associated with carnivores regularly results in small sample sizes and low detection probabilities (Long et al. 2011). To account for these potential pitfalls, camera-trap surveys, which can continuously sample with minimal disturbance, have proven an effective technique for monitoring carnivores (O'Connell et al. 2011). Furthermore, camera trap survey data are well suited for occupancy modeling that explicitly account for imperfect detections (MacKenzie et al. 2006). Habitat use is a dynamic process that can change with environmental variation, between seasons, and among years (Lendrum et al. 2017b). Therefore, the best way to reliably understand the ecological processes occurring within a system is to monitor it for prolonged periods, which has given rise to multiseason occupancy modeling (MacKenzie et al. 2006).

We analyzed data derived from camera traps using single-species multiseason occupancy modeling to assess carnivore community occurrence of coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and cougars (*Puma concolor*) relative to energy development infrastructure and natural landscape features in an energy extraction site in the Piceance Basin of northwestern Colorado. This area holds the second largest natural-gas reserve in the U.S. (Hawkins et al. 2016) and has been subject to periods of intensive development for the past several decades, resulting in high road density and energy production infrastructure. During the study, the Piceance Basin had transitioned to a production (natural-gas being extracted) phase. As a result, human activity and associated light and sound sources were reduced relative to the development phase. We examined seasonal drivers of carnivore habitat use with respect to development features associated with energy infrastructure and environmental variation during summer (June-Sept) and winter (Dec-March) seasons from 2014 – 2017.

Previous research in this study system has demonstrated that predation risk of mule deer (*Odocoileus hemionus*) by canid and felid predators increases further from producing well pads (Lendrum et al. 2017b) and that carnivores reduce their daytime activity in the presence of energy development (Lendrum et al. 2017a). Therefore, we hypothesized that carnivore habitat use would be reduced in proximity to energy development, resulting in negative associations between carnivore occupancy and development infrastructure. We also hypothesized that the magnitude of response would vary by species due to their differential sensitivity to disturbance (Crooks 2002). Specifically, we predicted that felids would be more responsive to energy development than coyotes, because felids often occur at naturally lower densities, exhibit increased wariness, and have more specialized habitat use and dietary requirements than coyotes, which show greater plasticity (Elbroch and Rinehart 2011). Further, we expected that cougars would show the greatest aversion to energy infrastructure given they are typically more sensitive to anthropogenic disturbances than are bobcats (Crooks 2002). A better understanding of how energy development that has transitioned into the production phase, which has the longest persistence on the landscape, influences carnivore habitat use can provide important information for wildlife conservation and aid in science-based management decisions.

METHODS

Study area

Within the Piceance Basin (39.924586° N, -108.197458° W), levels of natural-gas extraction vary markedly (Lendrum et al. 2012; Figure 3.1). The study area ranges in elevation from ~1,800 to 2,285 m, and is characterized by cold winters with most annual precipitation occurring as snowfall. Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) dominate the

woodlands, and big sagebrush (*Artemisia tridentata*) Utah serviceberry (*Amelanchier utahensis*), and bitterbrush (*Purshia tridentate*) are most common in the shrublands (Lendrum et al. 2014). Common species of large mammals include coyotes, bobcats, mule deer, and elk (*Cervus elaphus*), while cougars and black bears (*Ursus americanus*) occur with less frequency (Lendrum et al. 2017a). Notably, the Piceance Basin is a designated critical winter range for mule deer.

Study design

To quantify animal occurrence, we obtained data from 80 passive infrared RECONYX PC 800 digital cameras (Holmen, WI, USA) from 2014-2017 across the study area (Figure 3.1). Ten cameras were deployed during an initial winter and summer season, which was expanded to 80 cameras for the remaining 4 seasons. To provide adequate coverage, cameras were deployed in a systematic random design with each camera randomly placed within a 2 x 2 km grid across the entire study area at a minimum distance of $\geq$ 500 m between stations (Lendrum et al. 2017a). Cameras were placed as close as possible to each randomly chosen camera station, but near specific features expected to maximize capture probability, such as dirt roads, wildlife trails, and water sources (Lendrum et al. 2017a). Stations consisted of a single digital camera trap unit set on a tree at a height of approximately 40 cm, facing perpendicular to the expected direction of animal travel and approximately 3 m from the anticipated site of capture. All cameras were programed to include a date and time stamp to each photograph. Photographs were catalogued using Colorado Parks and Wildlife photo database (Newkirk 2014).

At each camera station, we sampled three natural landscape variables known to influence predator distributions (Hebblewhite et al. 2005; Elbroch et al. 2013) and four metrics of anthropogenic disturbance (Lendrum et al. 2017b). Natural landscape variables included habitat type (shrub or tree dominated), aspect (cosine transformed to represent Northness), and elevation

(m). Anthropogenic landscape features included distance to nearest producing well pad, road, pipeline, and industrial facility and years since the well pad was developed. We also measured the number of well pads and linear density of pipelines and roads within 500 and 1000 m buffers of each camera station. A detailed description of how variables were obtained are provided in Lendrum et al. (2017b). Additionally, we recorded 3 metrics thought to influence detection probability: whether the camera was set on a trail, the identity of the researcher that set the camera, and whether the field of view of the camera was obstructed by vegetation.

We divided each year into two seasons based on median migration dates of radio-collared mule deer (Lendrum et al. 2013), summer (June 1 - Sept 30) and winter (Dec 1 – March 31). We considered the carnivore population to be closed with no emigration or immigration within those seasons (Mackenzie et al. 2006). Within each season, a sampling occasion consisted of 5 days of camera photos for a total of 24 sampling occasions per season (Shannon et al. 2014). Because several of the target species have home ranges that can cover multiple stations, occupancy is better interpreted as the proportion of habitat "used" by the target species, and detection probability is the probability the species is present at the time of the survey and detected at occupied or used sites (Mackenzie et al. 2006; Lewis et al. 2015).

Carnivore occupancy

We used single-species multiseason occupancy modeling to estimate the initial occupancy (ψ; the proportion of the landscape used by the species in the first season), local colonization (γ; the probability that an unoccupied site in season t is occupied by the species in season $t + 1$), local extinction (ε; the probability that a site occupied in season t is unoccupied by the species in season $t + 1$), and detection probability (p; the probability of detecting a species given that it was present at a site) for each member of the carnivore community in relation to environmental

variables and features associated with anthropogenic disturbance (MacKenzie et al. 2006). We then examined seasonal trends in carnivore occupancy by deriving seasonal occupancy estimates via a recursive equation: $\Psi_t(1 - \varepsilon_t) + (1- \Psi_t) \gamma_t$, (MacKenzie et al. 2006).

We used a stepwise procedure to develop a candidate list of models reflecting biological hypotheses (Doherty et al. 2012; Bruggeman et al. 2016). First, we varied the predictor variables thought to influence *p* while holding Ψ, γ, ε at a 'general' model structure consisting of three variables (elevation, aspect, and habitat type). We then selected the best-supported structure for *p* by comparing the AICc value for each model. If multiple models received support (ΔAICc < 2; Burnham and Anderson 2002), we included the competing models in the next step of model selection. We then repeated this process for the Ψ, γ and ε, allowing each of the 10 variables to enter the model while retaining the best structures previously identified (Bruggeman et al. 2016). All model structures assessed in each step are provided in Appendices 1 and 2. We evaluated covariates from the top models on effect on Ψ, γ, ε and *p* based on the weight of evidence from the model table, and from the direction, magnitude, and 95% confidence intervals (CI) of the regression coefficient (Arnold 2010). All analyses were conducted in R (R Core Team, 2017) with the RMark package (Laake 2013) unless otherwise noted.

RESULTS

Across the 6 seasons, total sampling effort equated to 37,540 operating camera days (number of cameras * number of days operating) of the 40,800 camera days surveyed. We obtained over 8,000 photographs of our 3 target carnivores (coyote, bobcat, and cougar), including 4,702 photographs in summer and 3,483 photographs in winter. Coyotes were the most photographed carnivore (6,414), followed by bobcats (1,690) and cougars (81). All cameras obtained at least

one photograph of a carnivore during our survey. Coyotes were detected on 881 5-day sampling occasions and at 75 of the 80 camera stations, bobcats on 324 sampling occasions at 68 cameras, and cougars on 18 sampling occasions at 9 cameras. Because of the low number of cougar detections during the winter (n = 2), we were unable to effectively model multiseason cougar occupancy.

The best-supported model for habitat use by coyote included the number of well pads within 1 km of the camera (Ψ), elevation (γ and ε), and a seasonal effect (*p*) (Appendix 3.1). Initial coyote occupancy was best explained by the number of well pads within 1 km of the camera, with higher occupancy at low well pad densities ($\widehat{\Psi}$= 0.69, SE = 0.19 at an average of 2 well pads), with a decreasing trend in coyote occurrence as the number of well pads increased ($\hat{\beta}$ = -0.59, SE = 0.41 Figure 3.2a). The use of new sites across seasons (i.e., local colonization) by coyotes was more common at low elevations than at high elevations ($\hat{\beta}$ = -0.72, SE = 0.35; Figure 3.2b). The conversion of used to unused sites (i.e., local extinction) was also weakly related to elevation ($\hat{\beta}$ = -0.39, SE = 0.28; Figure 3.2c). Detection probability varied annually and was higher in summer (average $\hat{p}$ = 0.15, SE = 0.01) than winter (average $\hat{p}$ = 0.09, SE = 0.01; Figure 3.2d). Derived estimates of seasonal probability of occupancy from 2014-2017 ranged from 0.78 (SE = 0.7) to 0.84 (SE = 0.03; Figure 3.3).

Four models had similar support (Δ AIC <2) for best describing habitat use by bobcats (Appendix 3.2). Predictors of initial occupancy (Ψ) included well pad density and aspect, but also included the constant model with no variables (Appendix 3.2). All four models indicated habitat type was the best predictor of continued use (γ and ε), with seasonal variation in detection probability (*p*) (Appendix 3.2). Similar to coyote occupancy, the top supported model indicated that initial occupancy was best predicted by the number of wells within 1km of a camera, with

higher occupancy at low well pad density ($\widehat{\Psi}$ = 0.34, SE = 0.26 at an average of 2 well pads), and displayed a negative trend as the number of well pads increased ($\hat{\beta}$ = -0.94, SE = 0.88; Figure 3.4a). The use of new sites (i.e., colonization) was greater in woodland than in areas dominated by shrub cover ($\hat{\beta}$ = 0.33, SE = 0.45; Figure 3.4b). The conversion of used to unused sites (i.e., extinction) also varied with habitat type and was lower in woodlands ($\hat{\beta}$ = -1.04, SE = 0.48; Figure 3.4c). The probability of detecting a bobcat fluctuated seasonally with detection higher in summer (average $\hat{p}$ = 0.11, SE = 0.02) compared to winter ($\hat{p}$ = 0.05, SE = 0.01; Figure 3.4d). Derived estimates of seasonal bobcat occurrence were lower than for coyotes and ranged from 0.48 (SE = 0.06) to 0.52 (SE = 0.04; Figure 3.3).

DISCUSSION

Large intact landscapes, favorable to the persistence of wide ranging carnivores, are becoming less abundant as natural resource extraction and residential development escalate to accommodate human population growth (Crooks et al. 2017). As such, understanding how carnivore species persist in fragmented landscapes is of critical importance to carnivore conservation and management. In a production-phase natural gas field, the phase of development that has the lowest levels of human activity, we observed higher occupancy by bobcats and coyotes when well pad densities were at their lowest. While a decreasing trend in occupancy occurred at high well pad densities, there was large uncertainty in the estimates. Overall, coyote and bobcat occurrence were comparable to what has been observed in exurban developments in Colorado (Goad et al. 2014), though higher bobcat probabilities have been reported in Colorado populations that experienced little human persecution (Lewis et al. 2015). Cougars were detected

too infrequently to estimate occupancy, and were lower than would be expected based on extrapolated density estimates (Colorado Parks and Wildlife Cougar Management Plan 2004).

While research on urban ecology has indicated that coyotes are among the most adaptable mid- to large-carnivores (Gehrt 2010), they will preferentially use less developed (Goad et al. 2014) and larger habitat patches when available (Crooks 2002). In accordance, we detected higher habitat use by coyotes at levels of low well pad density. Furthermore, in the Piceance Basin, coyotes exhibited decreased activity in proximity to energy infrastructure during the day, even though human activity during the producing phase was relatively low (Lendrum et al. 2017a). Coyotes are heavily persecuted across their range, likely accounting for the observed reduction in diurnal activity and increased occurrence at lower levels of human development. Nevertheless, local declines in coyote populations are usually short term and regional populations remain stable (Bergstrom et al. 2014), which was consistent with the high levels of occupancy we observed by coyotes in the Piceance Basin throughout the duration of the study.

Bobcats are described as being sensitive to habitat fragmentation (Crooks 2002); therefore, we expected to detect a greater response by bobcats to energy infrastructure. As predicted, two of our four top models indicated higher habitat use by bobcats at low well pad density, although this effect was not as strong as for coyotes. Similar to coyotes, it is likely that bobcats are offsetting spatial displacement from energy development through a temporal response by reducing diurnal activity (Lendrum et al. 2017a). Habitat cover was a stronger predictor of multiseason habitat use, with bobcats more likely to occupy woodland than shrub cover. This finding is consistent with other research on bobcat occurrence in disturbed landscapes, where habitat use is greatest under forest cover (Goad et al. 2014), but inconsistent with previous research in the Piceance Basin where bobcats selected for areas with high shrub

cover (Gallo et al. 2016). However, Gallo et al. (2016) structured their sampling relative to woodland removal and did not sample across the broader landscape in areas with energy infrastructure.

The use of occupancy or detection to estimate density for broad-ranging species that may respond differently to anthropogenic disturbance is not recommended (Parsons et al. 2017); therefore, we did not attempt to estimate carnivore densities in this study. Nevertheless, occupancy estimates for bobcats in our system were substantially lower than occupancy estimates in other Colorado sites conducted under a comparable study design with similar topography, habitat, and prey composition, but which experienced little hunting or trapping (Lewis et al. 2015). Moreover, we did not expect the low detections of cougars, particularly during the winter months when predators and prey tend to be congregated (Elbroch et al. 2013). The larger 21,054 km^2 management unit has been identified by the state wildlife management agency as having potential for high cougar densities (2.0 – 4.6 lions/100 km^2) based on cougar habitat quality, and density estimates within our study area are thought to be in the upper portion of this range because of the high prey densities of deer and elk found on critical winter range habitat in the Piceance Basin (Colorado Mountain Lion Management Plan, 2004). However, in the 300 km^2 of mule deer winter range we surveyed, cougars were only detected twice in the winter, once in 2014 and again in 2017. Although cougar detections are a minimum value and do not account for missed detections, our results suggest that cougar densities in this portion of the management unit may be lower than expected.

The study design, particularly the fact that data collection occurred after the initiation of energy development, precludes conclusive determination if the observed low occurrence of felids is related directly to energy extraction activities, an associated disturbance such as harvest

pressure, or some other factor. Therefore, we pose two plausible hypothesis that could be tested by future studies where the collection of pre-disturbance data is possible. The first hypothesis is that disturbance-sensitive individuals emigrated from the study site to more suitable habitat, reducing the overall occurrence of felids on the landscape (Tuomainen and Candolin 2011). This could best be observed with radio telemetry, but could also be detected by changes in multiseason occupancy modeling as employed here.

An alternative hypothesis for the low occurrence of bobcats and cougars is a result of sport hunting and trapping pressure, which can affect population characteristics and distribution (Packer et al. 2009; Erb et al. 2012), particularly for low density carnivores such as wild felids. Furthermore, harvest pressure can be intensified in areas with high public access that would otherwise be remote, such as producing energy fields (Dorning et al. 2017). Specifically, the construction of roads to promote industrial expansion increases access for hunters, resulting in increased harvest (Trombulak and Frissell 2000). The Piceance Basin is composed almost entirely of public land with high road densities and receives more hunting and trapping pressure than private lands under similar conditions. Therefore, we were surprised by the low performance of road density as a predictor of carnivore occurrence; however, the median distance from a maintained or unimproved road is ~300 m in the Piceance Basin which provided little variation across camera stations.

The year prior to the initiation of our study, legal take of bobcats was the highest reported in the state over the past 15 years (1,945 bobcats; Colorado Parks and Wildlife Furbearer Report 2016), likely coinciding with particularly high prices for pelts of western bobcats. This demand, in conjunction with increased public access in our study area, may contribute to the relatively low occupancy we recorded for bobcats. Likewise, the number of cougars harvested in the

management unit the three years prior to the study nearly doubled from the preceding three years when the gas field was still actively being developed (23 to 40 cougars; Colorado Parks and Wildlife Mountain Lion Harvest Reports). We note that this harvest level was not inconsistent with the regional management objectives for a moderate suppression of cougars (15-20% harvest of the potential population) based on extrapolated densities. Wildlife managers across the Western U.S. are working towards improved methods for estimating cougar populations to better set management objectives (Robinson et al. 2015; Wolfe et al. 2016). Our findings corroborate the need for such information, particularly in human-dominated landscapes where development activities can increase human access reducing wildlife densities below that expected based solely on habitat quality.

The interactions between human development and wildlife responses are well studied, yet the magnitude of response varies greatly depending on the type of disturbance, level of intensity, and human use. The ability for carnivores to persist in such landscapes is largely dependent on the life-history characteristics and behavioral traits that make them more or less susceptible to habitat fragmentation, which can be compounded by human persecution, as evidenced in this study. Energy developments across the globe are transitioning into the producing phase when features become long term attributes of the landscape. Research such as this will help us understand how wildlife respond to human-dominated landscapes during times of low human density.

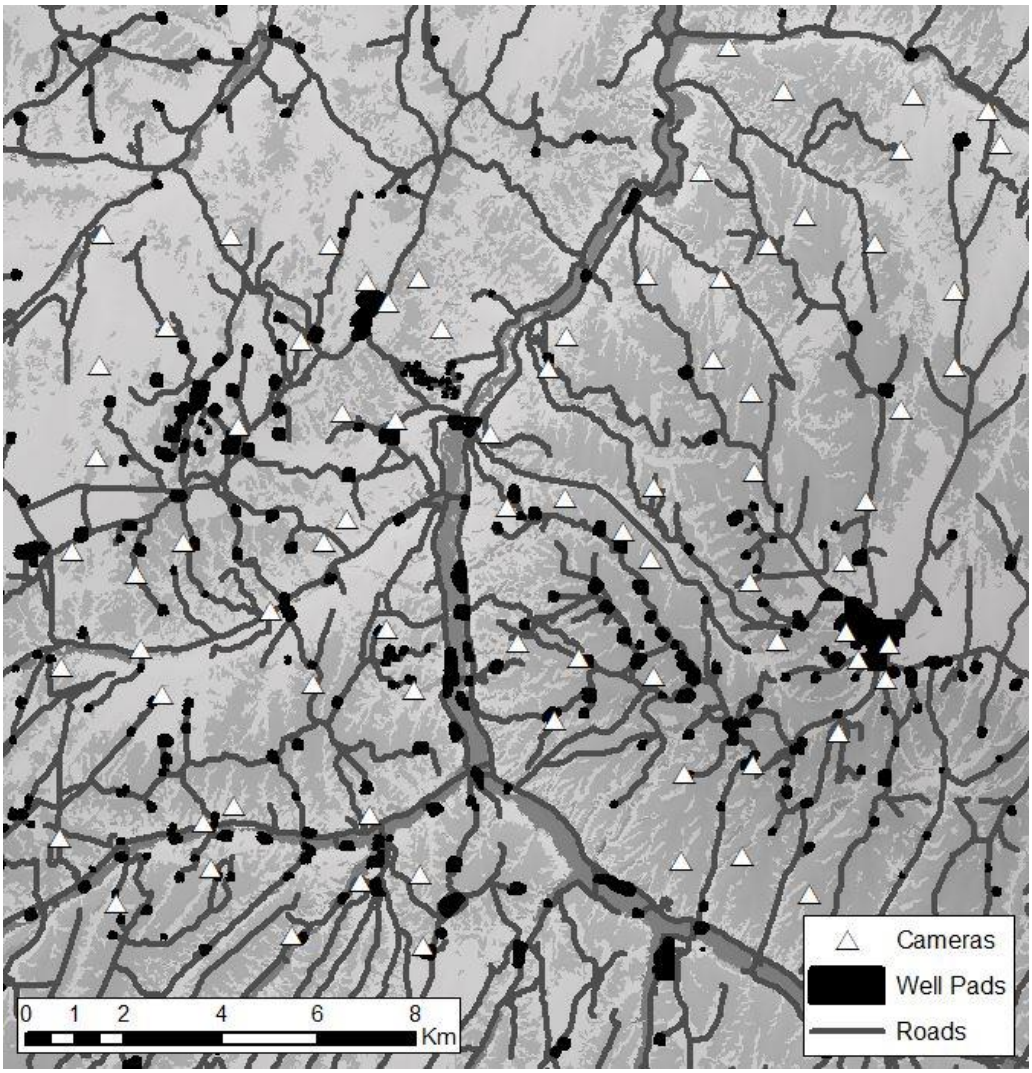

Figure 3.1. Location of camera traps, natural gas development infrastructure, and tree (dark shaded) or shrub (light shaded) dominated habitats in the Piceance Basin, CO, USA from 2014-2017.

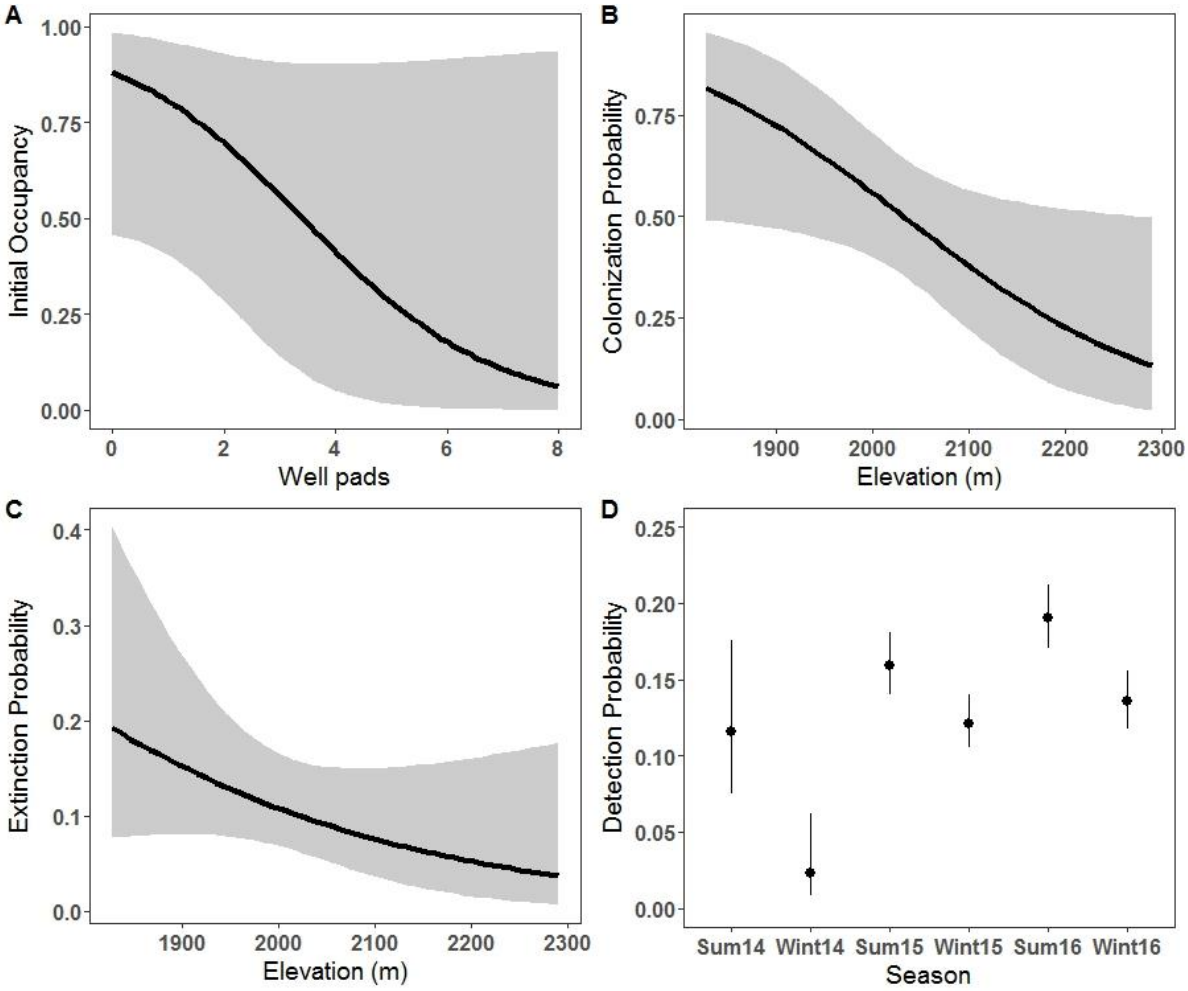

Figure 3.2. Probability of initial occupancy by coyotes related to well pad density within 1 km of the camera station (A), probability of local colonization (B) and extinction (C) with respect to elevation, and seasonal variation in detection (D) in the Piceance Basin, CO, USA, 2014-2017. Light grey bands depict upper and lower 95% CIs.

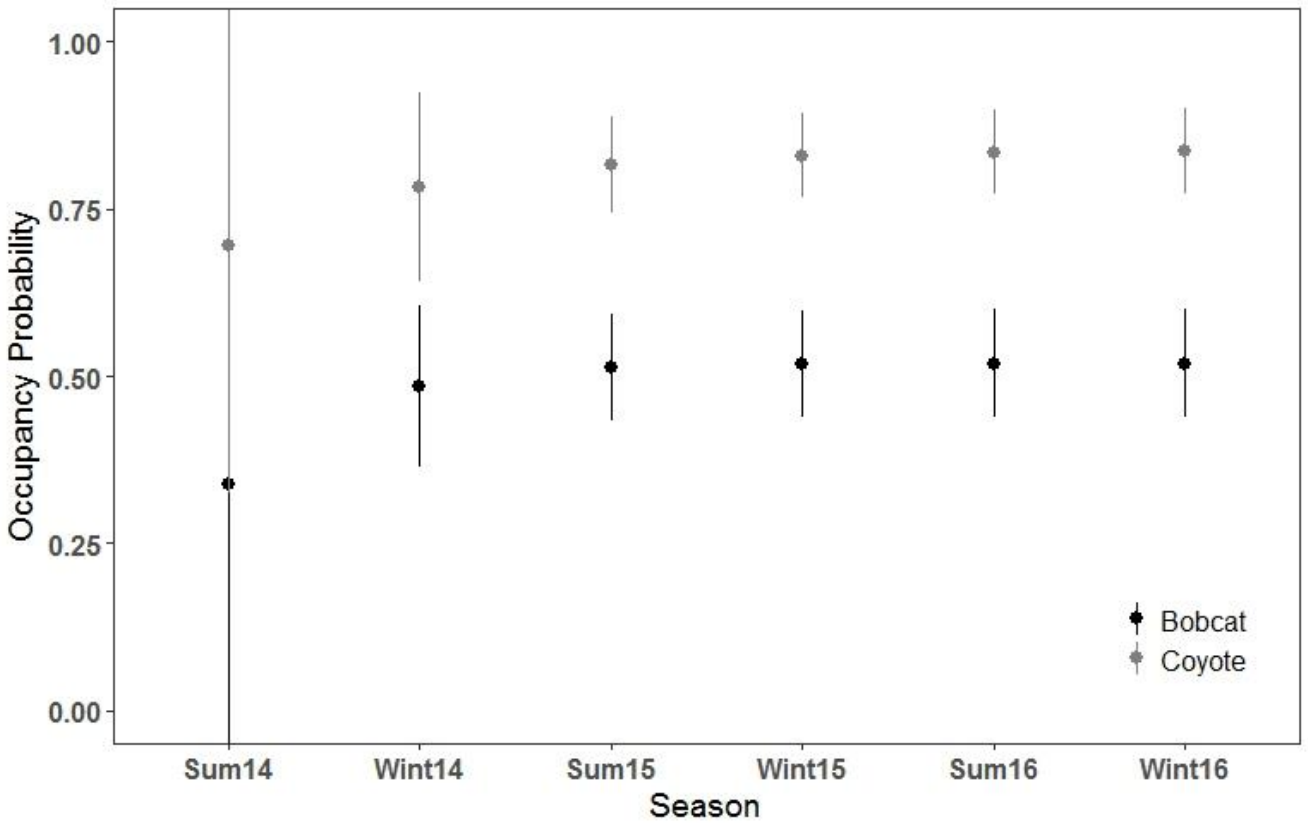

Figure 3.3. Derived summer (Sum) and winter (Wint) seasonal estimates of occupancy as predicted by top selected models for coyotes and bobcats in the Piceance Basin, CO, USA, 2014-2017.

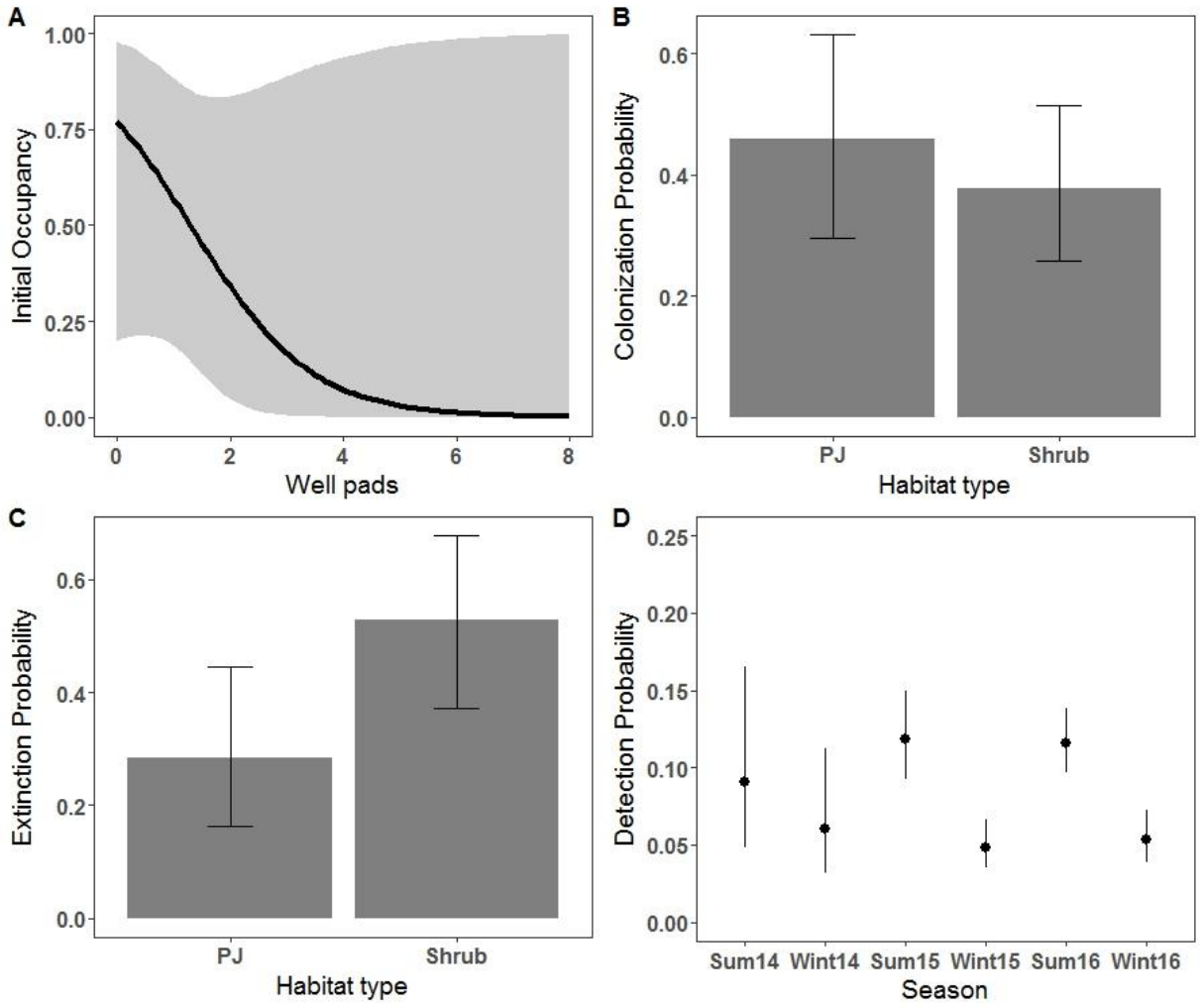

Figure 3.4. Probability of initial occupancy by bobcats related to well pad density within 1 km of the camera station (A), probability of local colonization (B) and extinction (C) with respect to pinyon-juniper and sagebrush habitats, and seasonal variation in detection (D) in the Piceance Basin, CO, USA, 2014-2017. Light grey bands depict upper and lower 95% CIs.

CHAPTER FOUR

HABITAT USE IN 'RISKY' ENVIRONMENTS: MESOCARNIVORE OCCURRENCE ACROSS A GRADIENT OF ANTHROPOGENIC DISTURBANCE IN PERIODS OF HIGH AND LOW PREY ABUNDANCE

INTRODUCTION

Optimal foraging provides a framework to conceptualize strategies employed by species when balancing predation risk with resource acquisition (Charnov 1976). Predictions stemming from this theoretical framework posit that animals will spend less time in habitats associated with greater risk if adequate resources are available in less risky environments (Brown 1988). Our understanding of animal habitat use and selection are rooted in this framework, which has served as the foundation for investigation of spatial dynamics in interspecific interactions (Pimm and Rosenzweig 1981). Risk can manifest lethally, in which a predation event occurs, or nonlethally, which can shape an organism's future decisions and habitat preference (Lima 1998). Whether animals display risk-averse or risk-pone behavior depends, in part, on the variance in risk associated with available habitat (Brown 1988).

Given the strong predatory role of humans in most systems (Darimont et al. 2015), human presence or disturbances often are perceived as predatory pressures, which can drive alterations in species interactions and habitat use related to human features and activities (Frid and Dill 2002). Perceiving anthropogenic disturbance as a risk source appears to be particularly strong in mammalian carnivores, to the degree where prey species may even use human features to avoid predation (Berger 2007). Human-modified landscapes also alter habitat characteristics

that may be of critical importance for predators (i.e., concealment cover for ambush predators), thereby increasing the risk of foraging in such habitats (Oriol-Cotterill et al. 2015). Furthermore, mammalian carnivores are often persecuted across their range, either because of competition for game or livestock or the perceived threat to humans, often resulting in increased risk to carnivores in landscapes with elevated human activity (Ordiz et al. 2013). Recent experimental studies have demonstrated that top predators (Smith et al. 2017) and mesocarnivores (Clinchy et al. 2016) respond negatively to the perceived presence of humans, resulting in reduced foraging behavior.

The niche breadth of a species can be used to predict how a species will respond to disturbance; more specialized species are expected to respond negatively to disturbance while generalist species may be more capable of coexisting in disturbed landscapes (specialization-disturbance hypothesis; Vázquez and Simberloff 2002). For example, obligate carnivores that rely heavily on few prey items, such as the dependence of bobcats (*Lynx rufus*) on lagomorphs (Dowd and Gese 2012, López-vidal et al. 2014), are often considered specialists species. In contrast, coyotes (*Canis latrans*), which display plasticity in their omnivorous diet and varied habitat use, are characteristic of a generalist predator (Larson et al. 2015). In accordance, coyotes tend to exploit human-dominated landscapes better than bobcats, which is particularly evident in urban systems (Crooks 2002, Riley et al. 2003) but has been less well documented in response to other forms of human disturbance.

Globally, resource extraction is a primary source of habitat conversion, most often resulting in negative impacts to terrestrial ecosystems and wildlife (Northrup and Wittemyer 2013). In North America, development for unconventional oil and gas is one of the principal drivers of land-use change and has increased in recent decades, resulting in over 3 million ha

occupied by oil and gas infrastructure in the U.S alone (Allred et al. 2015). The associated roads, pipelines, and well pads alter animal distributions and, in turn, interspecific interactions (Lendrum et al. 2018). As human disturbances continue to act as a non-random selective pressure favoring species best able to persist in modified landscapes (Smart et al. 2006), more research is needed regarding the effect of human disturbance on predator-prey interactions (Frid and Dill 2002).

Field experiments that use resource patches with variable predation risk are a valuable approach to examine the influence of predation on foraging behavior, habitat use, and interspecific interactions (Brown 1988). We examined spatiotemporal patterns of co-occurrence between predator (bobcat and coyote) and prey (rabbit) across a gradient of human disturbance (i.e., risk) in an actively producing natural-gas field. Using predictions of the risk-disturbance hypothesis (Frid and Dill 2002), we expected both mesocarnivore species to exhibit risk-averse habitat use in the presence of energy infrastructure, with reduced habitat use with increased human disturbance (i.e., well-pad density). However, as posited by the specialization-disturbance hypothesis (Vázquez and Simberloff 2002), we predicted that bobcats should display greater risk-sensitivity than coyotes to human disturbance. During the study, we observed a marked annual decline in the rabbit population, providing the opportunity to test this hypothesis across periods when the strength of interspecific interactions likely varied (Wiens 1989). We discuss how a better understanding of carnivore response to anthropogenic disturbance could inform science-based management decisions of predator populations (Artelle et al. 2018).

METHODS

Study area

The Piceance Basin of northwest Colorado, USA (39.924586° N, -108.197458° W) is designated critical winter range habitat for mule deer and the second largest natural-gas reserves in the U.S. (Martinez and Preston 2018). Within the basin, levels of natural-gas extraction vary markedly, leading to different densities of well pads and roads (Lendrum et al. 2012; Figure 4.1). The study area ranges in elevation from ~1,800 to 2,285 m and is characterized by cold winters with most annual precipitation occurring as snowfall. Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) dominate the woodlands, and big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), and bitterbrush (*Purshia tridentate*) are common in the shrublands. Common species of large carnivores include coyotes and bobcats, while cougars and black bears (*Ursus americanus*) occur with less frequency (Lendrum et al. 2017). Mule deer and elk are abundant in winter but exhibit seasonal migrations common of temperate regions (Lendrum et al. 2013). Smaller mammals included mountain cottontails (*Sylvilagus nuttallii*.), the occasional black-tailed jack rabbit (*Lepus californicus*), and various rodent species of which golden-mantled ground squirrels (*Callospermophilus lateralis*) and chipmunks (*Tamias sp.*) were most common (Lendrum et al. 2017).

Study design

To quantify animal occurrence, we obtained data from 80 passive infrared RECONYX PC 800 digital cameras (Holmen, WI, USA) from 2015-2016 across approximately 300 km^2 (Figure 1). Cameras remained at the same site for the duration of the study. To minimize the availability of alternative prey populations in the study area, we focused exclusively on summer seasons (June 1 - Sept 30), when mule deer migrate from the study area to higher elevations (Lendrum et al.

2012) and rabbits become the most abundant prey source. Within each summer season, we considered each day (24 hr period beginning at midnight) to be an occasion, such that each occupancy survey consisted of 122 occasions per season (Shannon et al. 2014).

To provide adequate coverage, cameras were deployed in a systematic random design with each camera randomly placed within a 2 x 2 km grid across the entire study area at a minimum distance of ≥ 500 m between stations (Lendrum et al. 2017). Cameras were placed as close as possible to each randomly chosen camera station, but near specific features expected to maximize capture probability, such as dirt roads, wildlife trails, and naturally occurring travel routes (Lendrum et al. 2017). Stations consisted of a single digital camera trap unit set on a tree at a height of approximately 40 cm, facing perpendicular to the expected direction of animal travel and approximately 3 m from the anticipated site of capture. All cameras were programed to include a date and time stamp to each photograph. Photographs were catalogued using Colorado Parks and Wildlife photo database (Ivan and Newkirk 2016).

We used the model structure identified as the top model for bobcat and coyote occurrence across the landscape (Lendrum et al. *in review*) to examine the combined effects of changes in relative prey abundance and anthropogenic disturbance. In the Piceance Basin, the number of well pads within 1,000 m of a camera was the best predictor of bobcat and coyote occurrence (Lendrum et al. *in review*). Locations of well pads were obtained from the Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/) and validated or corrected with National Agriculture Imagery Program aerial images (https://gis.apfo.usda.gov/arcgis/rest/services) from 2017.

Multispecies occupancy

We used single-season multispecies occupancy modeling (MacKenzie et al. 2006) to determine the probably of occupancy of species A (ψ^{A}; rabbit), and the probability of species B (bobcat or coyote) given species A is present (ψ^{BA}) for the 2015 and 2016 summer seasons. Specifically, we used the conditional two-species occupancy model, where species A is assumed to be dominant over species B, allowing for the incorporation of habitat covariates (Richmond et al. 2010). We consider rabbits to be the dominant species in this modeling framework because of the strong influence prey species have on predator distributions (Karanth et al. 2004). Bobcats and coyotes are highly mobile, have large home ranges, and one individual could be detected at multiple camera trap stations within one occasion; therefore, we interpreted occupancy as the proportion of habitat used by the given species (MacKenzie et al. 2006). In addition, we calculated species interaction factors (SIF) to identify if bobcats and coyotes were more likely to co-occur with rabbits than expected (SIF >1) or were independent of one another (SIF <1; Richmond et al. 2010). All occupancy analyses were conducted in R (R Core Team 2017) with the RMark package (Laake 2013).

Activity patterns

As an additional measure of the potential for co-occurrence and thus interspecific interactions between predator and prey, we fit kernel density functions to the temporal activity patterns of bobcats, coyotes, and rabbits, and estimated a coefficient of overlap between predator and prey for 2015 and 2016 (Schmid and Schmidt 2006, Ridout and Linkie 2009). Given bobcats are obligate carnivores that specialize on lagomorphs (Dowd and Gese 2012, López-vidal et al. 2014), we expected greater temporal overlap between bobcats and rabbits compared to that between coyotes and rabbits. To estimate 95% confidence intervals from which to draw

inference (Arnold 2010), we generated 10,000 random smoothed bootstrap samples from the kernel density estimated from the original data and estimated a coefficient of overlap for each paired sample (Ridout and Linkie 2009). Only photographs that were obtained >1 hr apart were used in the analyses (independent events; Lendrum et al. 2017) to prevent artificially inflated sample sizes. The total number of independent photographs also were used as an index of relative rabbit abundance from one year to the next. All activity analyses were conducted with Overlap package (Meredith and Ridout 2017), again in R.

RESULTS

Total sampling effort during the summer of 2015 and 2016 equated to 9,640 and 9,739 operating camera days (number of cameras * number of days operating) respectively. In 2015, cameras captured 2,237 independent photographs of rabbits at 67 camera sites, 107 bobcat photographs at 28 sites, and 361 coyote photographs at 58 sites (Figure 4.2). In 2016, the number of independent photographs of rabbits declined by 75% to 545 at 52 sites, photographs of bobcats increased by 41% to 152 at 51 sites, and photographs of coyotes increased by 17% to 425 at 58 sites (Figure 4.2). Rabbits and coyotes were detected across all well pad densities in both years; bobcats were not detected at the highest well pad densities in 2015, but at all densities in 2016 (Figure 4.2).

Occupancy of rabbits at the average well pad density (2.2 well pads within 1,000 m of a camera station) was higher in 2015 (0.85 ± SE 0.04) compared to 2016 (0.69 ± 0.05; Figure 4.3) and was not strongly influenced by the number of well pads in either year (Table 4.1; Figure 4.3). At high relative rabbit abundance (2015), the co-occurrence of bobcat and rabbits was highly interrelated (SIF =1.17, 95% CI = 1.06-1.28); this co-occurrence remained similar as rabbits declined in 2016 (SIF = 1.15, 95% CI = 0.96-1.35). In 2015, bobcats had a high

probability of co-occurrence with rabbits at low well pad densities, which declined significantly as well pad densities increased (Table 4.1; Figure 4.3). Conversely, in 2016 when relative rabbit abundance was lower, the co-occurrence of bobcats and rabbits remained high regardless of well pad densities (Table 4.1; Figure 4.3).

The probability of coyote occupancy given a rabbit was present was relatively high and stable in both 2015 and 2016 (Figure 4.3), but coyotes were less likely than bobcats to co-occur with rabbits during both years (2015: SIF =0.98, 95% CI = 0.96-1.0; 2016: SIF = 0.98, 95% CI = 0.92-1.05). Well pad density was not a strong predictor of the probability of coyotes co-occurring with rabbits during years of low or high rabbit abundance (Table 4.1), though greater uncertainty in our estimates existed at higher well pad densities (Figure 4.3).

Bobcats displayed a high degree of overlap in activity patterns with rabbits in 2015 (Δ = 0.82, 95% CI = 0.75-0.89), which was unchanged as rabbit abundance declined in 2016 (Δ = 0.82, 95% CI = 0.75-0.89; Figure 4.4A). As predicted, coyotes displayed less overlap with rabbits than did bobcats in 2015 (Δ = 0.73, 95% CI = 0.68-0.77), which further decreased in 2016 (Δ = 0.67, 95% CI = 0.61-0.72; Figure 4.4B).

DISCUSSION

The functional relationship between predator distribution and prey density is a principle driver of community structure (Carbone and Gittleman 2002, Karanth et al. 2004); however, this relationship can be altered in the presence of anthropogenic disturbance when perceived as risk (Frid and Dill 2002). We examined habitat use of a generalist and specialist carnivore across a gradient of human-caused disturbance during periods of high and low prey abundance to assess potential changes in risk tolerance associated with resource availability. We observed that when

relative rabbit abundance was high, bobcats, an obligate carnivore, had less probability of using habitat in areas of high human disturbance, indicative of risk-averse habitat use and consistent with the risk disturbance hypothesis (Frid and Dill 2002). However, when relative rabbit abundance declined by 75% in 2016, bobcat habitat use increased in areas of high human disturbance given prey was present, highlighting the potential importance of prey availability in determining predator distribution. Coyotes, a generalist predator, did not display strong differences in habitat use in response to the combined effects of prey abundance and anthropogenic disturbance. These findings are consistent with the specialization-disturbance hypothesis that predicts specialist species are more vulnerable to disturbance than their generalist counterparts (Vázquez and Simberloff 2002).

The spatiotemporal distributions of wildlife are patterned to meet the necessary requirements for continued survival (e.g., foraging), and specialization in interspecific interactions is expected to strengthen these patterns (MacArthur 1955). In addition to the tightly coupled spatial co-occurrence between bobcats and rabbits, temporal activity patterns of bobcats were more closely matched to those of rabbits than between coyotes and rabbits, providing further support of bobcats as obligate carnivores with lagomorphs as a primary prey (Dowd and Gese 2012, López-vidal et al. 2014), compared to the dietary and habitat plasticity displayed by coyotes (Larson et al. 2015). Additionally, when competition with coyotes exists, the proportion of lagomorphs in the diet of bobcats has been shown to increase (Litvaitis and Harrison 1989). Rather than prey limitation being responsible for the observed increase in habitat use by bobcats at higher well pad densities, it is conceivable the result was from an increase in the overall bobcat population across the landscape, as suggested by elevated camera detections in 2016. However, we suspect this is unlikely, because no change was detected in the overall occurrence of bobcats

from 2014-2017 in this system, which has a lower occurrence of bobcats than reported elsewhere in Colorado (Lendrum et al. *in review*). Instead, we postulate that increased bobcat detections at cameras with high well pad densities in 2016 were because bobcats increased their home range size and possibly movement rates in response to reduced prey availability (Litvaitis et al. 2016). We acknowledge that with only two seasons of contrasting rabbit abundance across one study area, we were unable to provide any replicate analyses, and therefore our findings should be interpreted as such.

Counter to the specialization-disturbance hypothesis, it could instead be hypothesized that because generalist species display plasticity in their diet and could theoretically switch to alternative food sources away from danger, they too should exhibit risk-averse behavior (Brown 1988). However, we did not find strong evidence for risk-aversive behavior in coyotes in relation to energy development, with only a weak decline in coyote occupancy at high well pad density. In urban settings, the availability of anthropogenic food subsidies (e.g., cultivated fruits and vegetables, trash, domestic pets) can help support high densities of coyotes (Fedriani et al. 2001), but this is typically not the case in actively producing energy fields. Perhaps coyotes are using developed habitats because human activity is relatively low during the production phase, when the study was conducted, thus reducing the threat of persecution; whereas, bobcats are more wary of human disturbance in general, or may be more reliant on vegetative structure that is reduced at high well pad densities.

In fact, the risks associated with foraging and habitat use in human-dominated landscapes are likely a combination of factors, including altered prey availability (Berger 2007, Oriol-Cotterill et al. 2015) and persecution by humans (Ordiz et al. 2013). Coyotes and bobcats are hunted and trapped across much of their range, increasing risk in non-urban human-dominated

landscapes. In the U.S., energy expansion into rural landscapes often occurs on public land and greatly increases human hunter access via the extensive road network associated with energy development (Dorning et al. 2017), and well pad and road density are highly correlated in the Piceance Basin ($r > 0.60$). For mammalian carnivores that are wide-ranging, naturally occur at lower densities then their prey, and have a propensity for human-wildlife conflict, a better understanding of habitat use under various conditions, including changes in prey density and human disturbance, is of critical importance for science-based management of hunted species in human-modified landscapes (Artelle et al. 2018).

Our results suggest that resource limitations homogenized the responses of generalist and specialist species to human-disturbed habitats by increasing bobcat habitat use in disturbed landscapes, thereby, increasing the possibility for interactions with humans. With the combined use of noninvasive camera traps (O'Connell et al. 2011) and multispecies occupancy modeling (Mackenzie et al. 2006), we provided empirical support for the specialization-disturbance hypotheses (Vázquez and Simberloff 2002). As conservation practitioners prepare for greater human-induced habitat alteration and changing environmental conditions, the combined use of theoretical ecology and empirical studies can provide valuable information to further conservation efforts.

Table 4.1. Parameter estimates for the number of well pads within 1 km of a camera station used to predict the probability of occupancy (ψ) by rabbits, bobcats given rabbits were present (Bobcat:Rabbit), and coyotes given rabbits were present (Coyote:Rabbit) in the Piceance Basin, Colorado USA, during periods of high (2015) and low (2016) rabbit abundance.

	2015				2016			
			95% CI				95% CI	
	β	SE	Lower	Upper	β	SE	Lower	Upper
ψRabbit	-0.10	0.13	-0.36	0.16	-0.07	0.11	-0.28	0.14
ψBobcat:Rabbit	-0.45	0.14	-0.73	-0.17	0.02	0.18	-0.33	0.37
ψCoyote:Rabbit	-0.21	0.15	-0.50	0.08	-0.22	0.26	-0.74	0.29

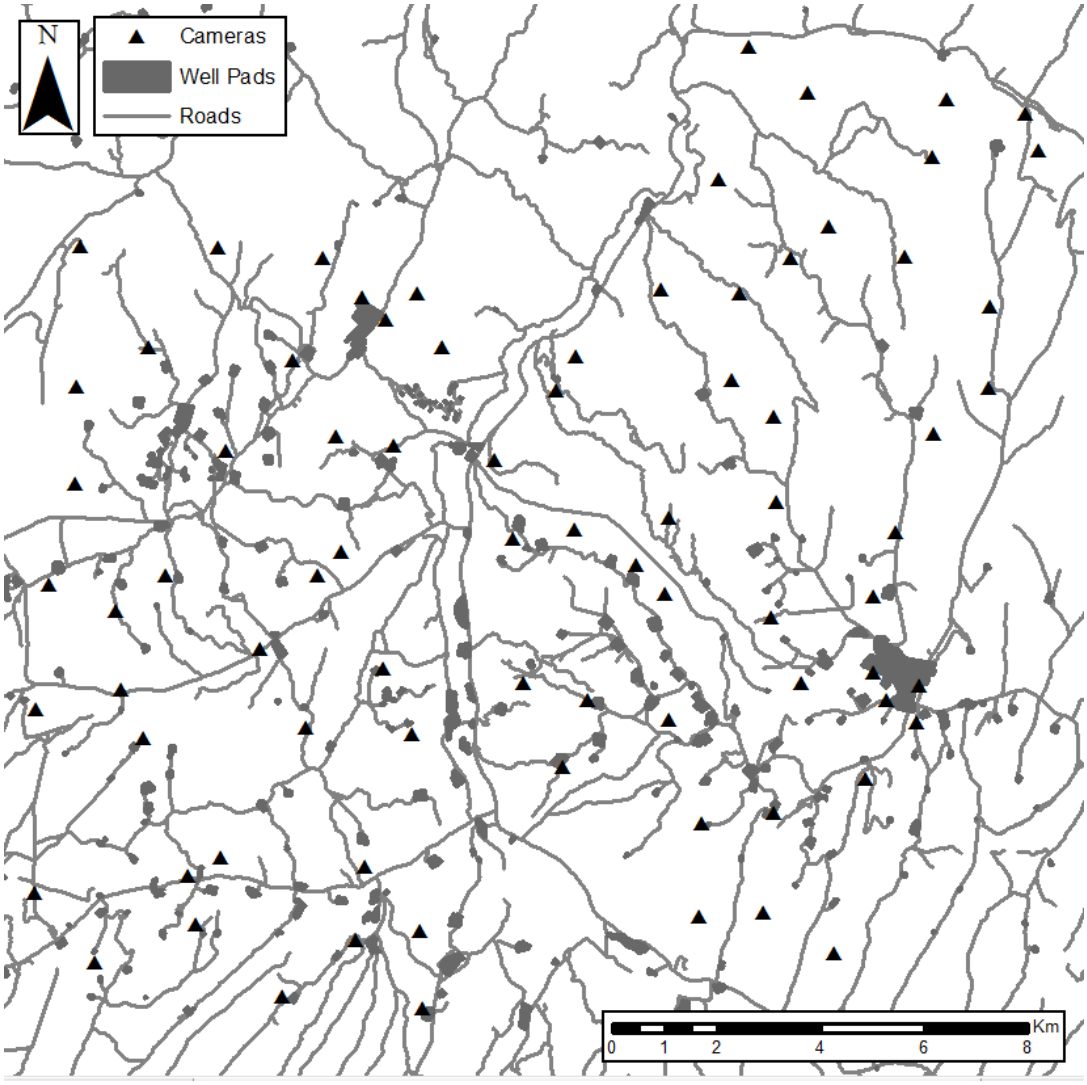

Figure 4.1. Placement of 80 camera traps in relation to roads and well pads, in the Piceance Basin, CO, USA, 2015-2016.

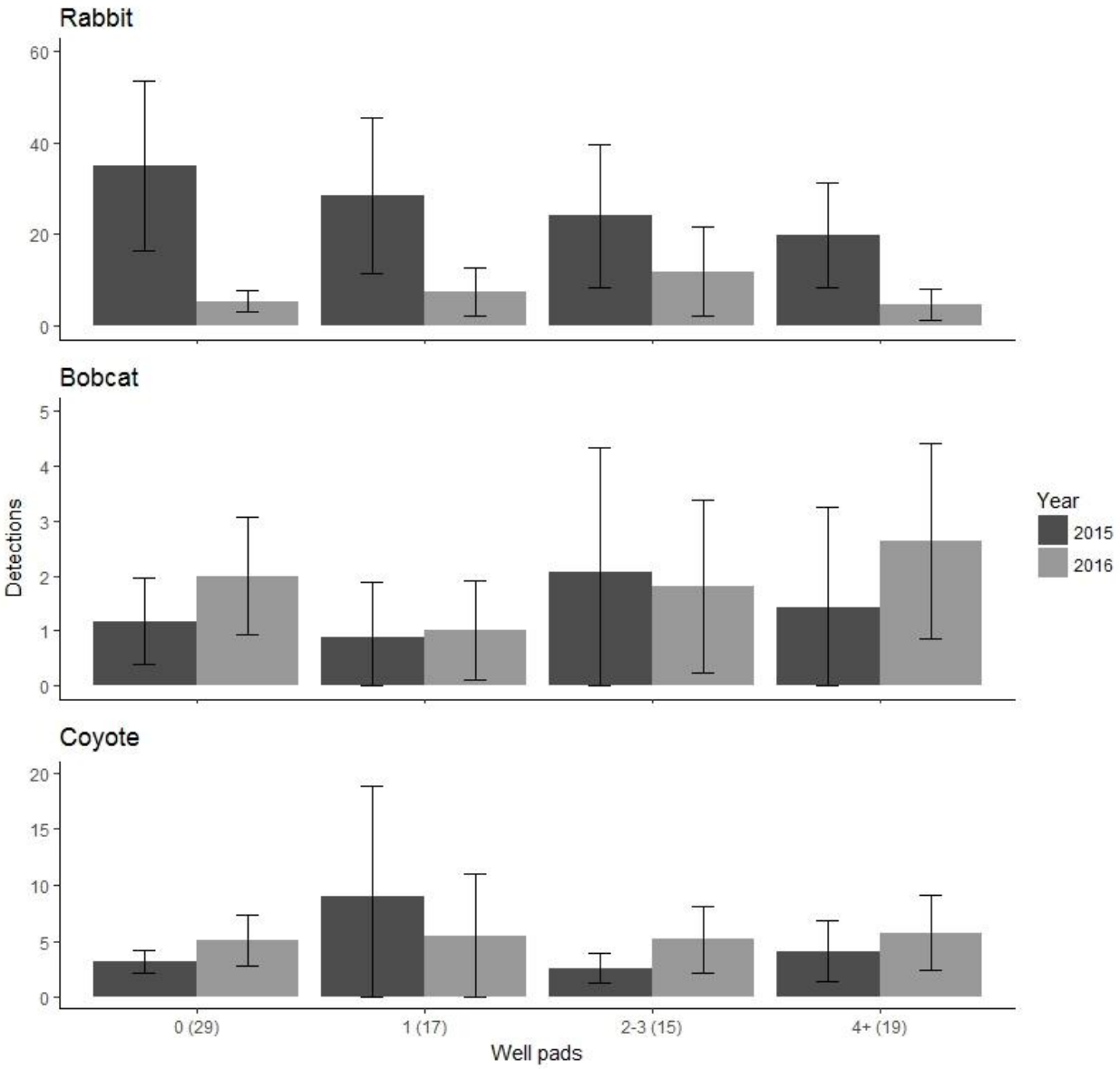

Figure 4.2. The average number of independent photographs of rabbits, bobcats, and coyotes per camera with 0, 1, 2-3, and 4+ well pads within 1 km of the camera, from June through September 2015 and 2016 in the Piceance Basin, CO USA. Numbers inside the parentheses indicate the number of cameras in each bin. Error bars are 95% confidence intervals.

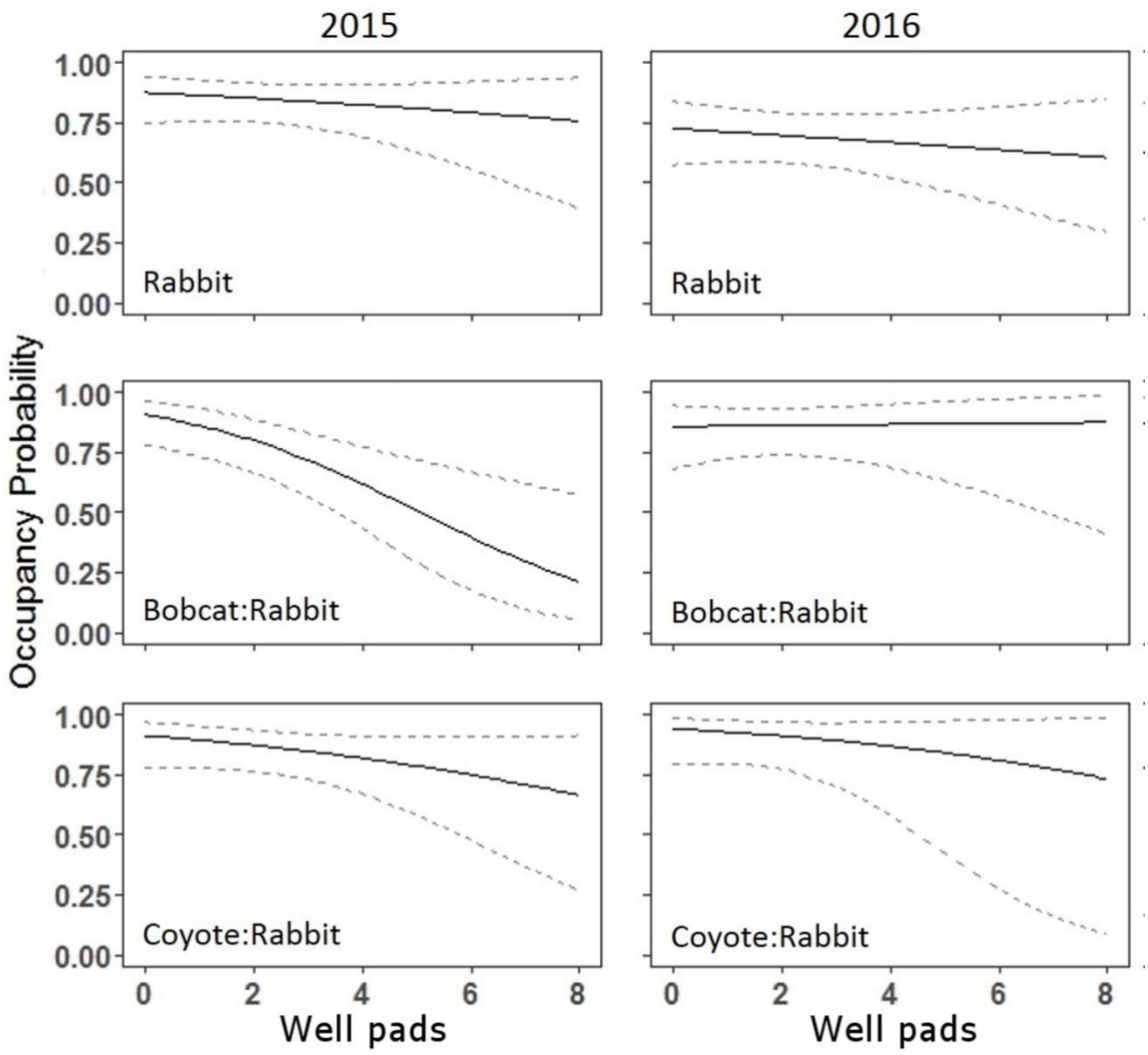

Figure 4.3. Probability of occupancy for rabbits, bobcats given a rabbit was present (Bobcat: Rabbit), and coyotes given a rabbit was present (Coyote: Rabbit) across a gradient of well pad densities within 1 km of the camera station in the Piceance Basin, USA, 2015 and 2016.

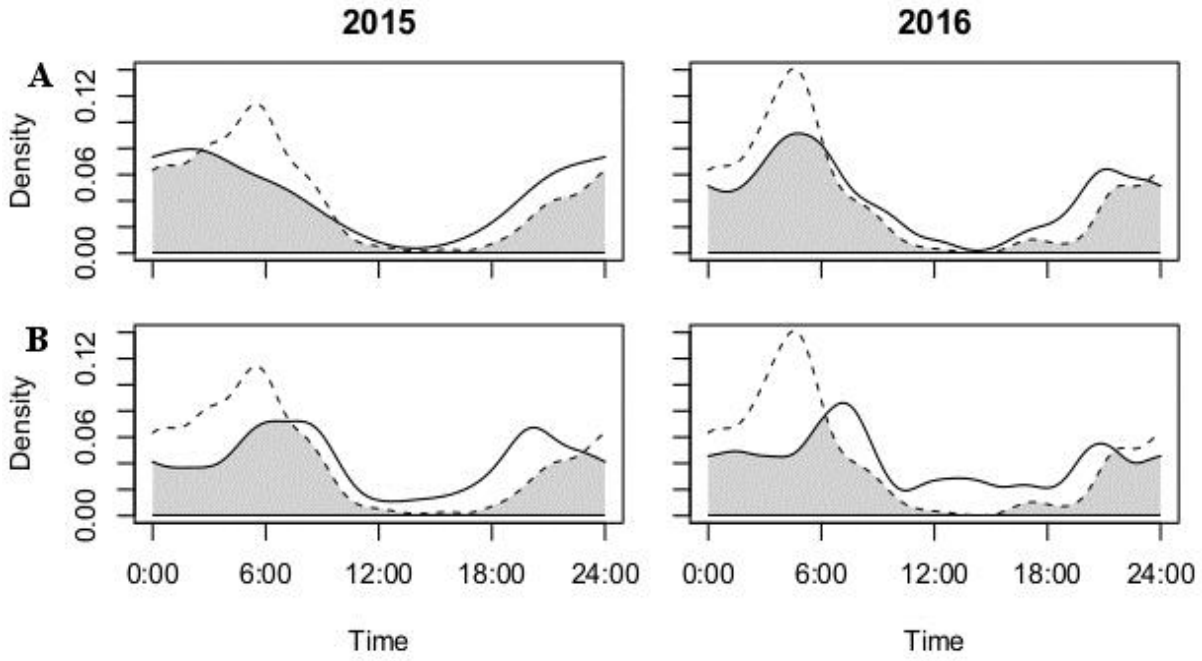

Figure 4.4. Kernel density functions fit to the temporal activity patterns of bobcats (A) and coyotes (B) in solid lines and rabbits in dashed lines, and the estimated coefficient of overlap (shaded grey) in the Piceance Basin, USA, 2015 and 2016.

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APPENDIX 1.1

Descriptive statistics of variables examined in predation site selection, GPS deer locations, and random locations in the undeveloped area, and developed area during the periods of high and low development: terrain ruggedness (VRM), snow depth; and distance to: ecotone edge (between forest and shrubs), drilling well pads, producing well pads, pipelines, secondary roads, primary roads, and industrial facilities during the winter in the Piceance Basin, CO, USA, 2008-2014.

Variable and Site	Predation sites				
	Mean	SD	Median	Min	Max
VRM					
Undeveloped high	0.14	0.16	0.05	0.00	0.81
Developed high	0.16	0.19	0.08	0.00	0.83
Undeveloped low	0.13	0.20	0.05	0.00	0.55
Developed low	0.11	0.15	0.05	0.00	0.77
Snow					
Undeveloped high	0.18	0.10	0.18	0.00	0.43
Developed high	0.13	0.11	0.12	0.00	0.41
Undeveloped low	0.13	0.14	0.14	0.00	0.32
Developed low	0.10	0.09	0.08	0.00	0.27
Ecotone edge					
Undeveloped high	65.17	134.93	32.31	0.45	352.61

Developed high	70.26	92.49	32.65	0.25	607.58
Undeveloped low	101.28	83.80	38.76	2.51	514.38
Developed low	83.48	87.68	57.74	1.26	333.43
Drilling					
Undeveloped high	6331.80	2701.54	6058.32	448.09	15771.92
Developed high	3124.40	2101.95	2735.89	323.62	14054.96
Undeveloped low	7666.85	3439.06	7262.23	3615.77	14971.30
Developed low	4010.60	2416.28	3849.84	338.27	14294.39
Producing					
Undeveloped high	2048.32	711.34	2107.70	371.16	3777.16
Developed high	900.09	624.52	744.45	139.13	3413.36
Undeveloped low	1910.86	907.21	1953.20	368.16	3555.12
Developed low	770.79	536.32	609.28	69.63	2628.22
Pipeline					
Undeveloped high	776.50	498.62	653.04	9.50	2111.87
Developed high	282.12	256.96	232.98	1.10	1269.54
Undeveloped low	608.68	545.52	415.73	7.73	1949.02
Developed low	304.95	282.73	210.03	1.67	1419.86
Major roads					
Undeveloped high	846.14	637.41	686.51	2.63	2434.72
Developed high	779.70	719.22	540.48	4.46	3294.76
Undeveloped low	785.63	604.61	643.51	9.57	2771.02

Developed low	740.87	799.45	447.69	1.98	3635.37
Secondary roads					
Undeveloped high	363.54	284.54	310.34	0.36	1059.48
Developed high	271.88	218.56	220.21	18.20	1062.04
Undeveloped low	409.60	255.35	404.07	3.62	1334.09
Developed low	231.96	178.25	184.70	1.32	708.40
Facility					
Undeveloped high	3235.66	1423.33	3294.92	342.50	5639.30
Developed high	1403.26	874.84	1201.55	62.06	3972.16
Undeveloped low	3192.57	1349.71	3037.51	503.75	5703.94
Developed low	1558.03	1387.55	1146.16	0.00	9491.87

Variable and Site	GPS locations					Random locations				
	Mean	SD	Median	Min	Max	Mean	SD	Median	Min	Max
VRM										
Undeveloped high	0.12	0.16	0.05	0.00	0.97	0.12	0.16	0.05	0.00	0.96
Developed high	0.14	0.17	0.07	0.00	0.98	0.13	0.17	0.06	0.00	0.99
Undeveloped low	0.10	0.15	0.04	0.00	0.96	0.12	0.16	0.05	0.00	0.97
Developed low	0.14	0.17	0.06	0.00	0.98	0.13	0.16	0.05	0.00	0.97
Snow										
Undeveloped high	0.14	0.13	0.11	0.00	0.56	0.15	0.15	0.11	0.00	0.70
Developed high	0.10	0.12	0.05	0.00	0.66	0.11	0.13	0.05	0.00	0.72

Undeveloped low	0.14	0.11	0.14	0.00	0.48	0.12	0.11	0.12	0.00	0.53
Developed low	0.09	0.09	0.07	0.00	0.51	0.09	0.09	0.07	0.00	0.51
Ecotone edge										
Undeveloped high	95.38	139.72	39.13	0.00	888.22	80.95	117.20	34.42	0.00	882.31
Developed high	59.78	69.55	35.14	0.00	572.29	62.43	72.73	35.90	0.00	572.29
Undeveloped low	135.05	163.96	60.05	0.00	888.26	88.54	124.70	37.01	0.00	880.54
Developed low	70.69	105.77	34.24	0.00	888.26	73.92	96.18	38.75	0.00	892.46
Drilling										
Undeveloped high	6019.83	3011.92	5977.01	12.70	16956.21	6948.43	3778.29	6368.57	0.00	20034.27
Developed high	3099.77	2043.91	2687.90	12.70	13972.06	3392.38	2362.91	2960.34	0.00	15142.33
Undeveloped low	7041.10	3004.90	6626.15	2315.50	18818.39	8707.96	3442.48	8223.15	2227.08	20061.12
Developed low	4177.49	1703.10	4241.07	24.28	15560.62	4878.73	2959.76	4307.75	0.00	16584.55
Producing										
Undeveloped high	1919.59	922.08	1915.77	0.00	4665.89	1997.03	969.19	1946.73	0.00	5899.32
Developed high	811.67	549.48	703.10	0.00	3942.03	875.58	630.07	732.44	0.00	4060.29
Undeveloped low	1539.78	886.87	1438.01	0.00	5874.71	1783.95	847.79	1772.80	0.00	4384.02
Developed low	707.51	511.63	597.76	0.00	3137.18	764.93	582.39	620.87	0.00	3192.67
Pipeline										
Undeveloped high	572.03	495.06	422.50	0.02	2389.88	723.18	564.38	607.44	0.00	2682.67
Developed high	245.86	228.83	177.88	0.00	2317.40	308.19	323.28	210.17	0.00	2339.81
Undeveloped low	491.17	488.59	307.00	0.00	2215.53	622.98	507.60	502.92	0.00	2651.97
Developed low	263.89	271.41	180.70	0.00	2307.43	320.80	331.53	214.90	0.00	2351.55

Major roads										
Undeveloped high	849.64	724.96	602.85	0.01	3567.30	838.22	701.99	643.98	0.01	3566.77
Developed high	818.90	780.65	573.93	0.04	3966.31	772.17	726.19	570.97	0.00	3960.79
Undeveloped low	958.98	816.06	652.24	0.18	3617.54	842.17	677.49	670.20	0.00	3610.51
Developed low	1120.16	965.15	831.17	0.10	3973.88	768.45	775.94	517.13	0.00	3972.81
Secondary roads										
Undeveloped high	342.96	240.44	292.67	0.08	1404.54	395.97	295.21	331.80	0.02	1534.66
Developed high	255.09	203.06	205.27	0.01	1469.24	282.79	230.36	230.02	0.00	1448.41
Undeveloped low	335.28	253.06	271.75	0.01	1535.11	396.14	299.88	328.12	0.01	1547.32
Developed low	243.02	185.34	200.87	0.00	1285.11	267.73	212.80	222.33	0.01	1443.84
Facility										
Undeveloped high	3277.58	1556.52	3732.28	0.00	6338.56	3251.22	1413.97	3366.41	0.00	6414.72
Developed high	1529.79	903.20	1401.02	0.00	4677.28	1598.26	956.65	1457.77	0.00	4670.36
Undeveloped low	2574.79	1394.76	2477.69	0.00	5777.28	3256.40	1355.71	3279.07	0.00	6381.30
Developed low	1869.25	1123.11	1683.85	0.00	9482.86	1887.25	1637.64	1480.01	0.00	10630.29

APPENDIX 1.2

Interpretation of resource selection function (RSF) and latent selection difference function (LSDF) for three different categories of covariates: binary (or categorical) such as habitat type; position-based such as snow depth, terrain ruggedness; proximity-based such as distance to ecotone edge or distance to nearest road

Coefficient	RSF	LSDF
Binary covariates		
+	greater than expected at random	greater than prey distribution
-	less than expected at random	less than prey distribution
=	at random	equal to prey distribution
Position based covariates		
+	higher than expected at random	higher than prey distribution
-	lower than expected at random	lower than prey distribution
=	at random	equal to prey distribution
Proximity based covariates		
+	further than expected at random	further than prey distribution
-	closer than expected at random	closer than prey distribution
=	at random	equal to prey distribution

APPENDIX 3.1

Stepwise model selection process for probability of initial occupancy (Ψ), extinction (ε), colonization (γ), and detection (*p*) of coyotes in the Piceance Basin, CO, USA, 2014-2017. The top model is in bold. Predictor variables for *p* included a seasonal effect (Season), which researcher placed the camera (Set by), if the camera was on or off trail (Trail), a model with no variables (Null), if the field of view was partially obstructed or not (FOV), and variation among survey (Survey). Predictor variables for Ψ, ε, and γ included a general model structure which including elevation, aspect and habitat type (General), the number of producing well pads and the density of roads and pipelines within 1km ("Feature type" 1 km) and 500 m ("Feature type" 500 m) of the camera, time since the closest well pad was drilled (Well years), distance to the nearest well pad (Well pad), industrial facility (Facility), pipeline (Pipeline), road (Road), habitat type (Habitat), elevation (Elevation), and aspect (Aspect).

Ψ	ε	γ	*p*	k	AIC*c*	Δ AIC*c*	*w*	Deviance
Step1								
General	General	General	Season	18	5203.80	0.00	0.63	5165.58
General	General	General	SetBy	14	5205.03	1.23	0.34	5175.68
General	General	General	Trail	14	5210.13	6.33	0.03	5180.78
General	General	General	Null	13	5242.47	38.67	0.00	5215.31
General	General	General	FOV	14	5244.19	40.39	0.00	5214.84
General	General	General	Survey	36	5256.72	52.92	0.00	5175.53
Step 2								

Wells 1 km	General	General	Season	16	5196.09	0.00	0.32	5162.34
Wells 1 km	General	General	Set by	12	5198.62	2.53	0.09	5173.63
Well pad	General	General	Season	16	5199.19	3.10	0.07	5165.44
Null	General	General	Season	15	5199.57	3.47	0.06	5168.02
Habitat	General	General	Season	16	5200.69	4.60	0.03	5166.94
Roads 1 km	General	General	Season	16	5200.85	4.75	0.03	5167.09
Null	General	General	Set by	11	5200.90	4.80	0.03	5178.06
Well pad	General	General	Set by	12	5201.00	4.90	0.03	5176.00
Facility	General	General	Season	16	5201.15	5.06	0.03	5167.40
Pipeline	General	General	Season	16	5201.27	5.17	0.02	5167.51
Elevation	General	General	Season	16	5201.29	5.20	0.02	5167.54
Pipelines 1 km	General	General	Season	16	5201.62	5.53	0.02	5167.87
Aspect	General	General	Season	16	5201.63	5.53	0.02	5167.87
Habitat	General	General	Set by	12	5201.65	5.55	0.02	5176.65
Roads 1 km	General	General	Season	16	5201.70	5.61	0.02	5167.94
Wells 500 m	General	General	Season	16	5201.75	5.65	0.02	5167.99
Well years	General	General	Season	16	5201.75	5.66	0.02	5168.00
Roads 500 m	General	General	Season	16	5201.78	5.68	0.02	5168.02
Pipelines 500 m	General	General	Season	16	5201.78	5.68	0.02	5168.02
Roads 1 km	General	General	Set by	12	5202.06	5.96	0.02	5177.06
Pipeline	General	General	Set by	12	5202.53	6.43	0.01	5177.53
Aspect	General	General	Set by	12	5202.72	6.63	0.01	5177.73

Elevation	General	General	Set by	12	5202.76	6.67	0.01	5177.77
Facility	General	General	Set by	12	5202.83	6.74	0.01	5177.84
Road	General	General	Set by	12	5202.91	6.82	0.01	5177.92
Pipelines 1 km	General	General	Set by	12	5202.97	6.87	0.01	5177.97
Well years	General	General	Set by	12	5202.97	6.88	0.01	5177.98
Roads 500 m	General	General	Set by	12	5203.00	6.91	0.01	5178.01
Wells 500 m	General	General	Set by	12	5203.04	6.95	0.01	5178.05
Pipelines 500 m	General	General	Set by	12	5203.05	6.96	0.01	5178.06
Step 3								
Wells 1 km	Elevation	Elevation	Season	12	5196.24	0.00	0.59	5171.25
Wells 1 km	Habitat	Habitat	Season	12	5199.17	2.93	0.14	5174.18
Wells 1 km	Null	Null	Season	10	5200.74	4.49	0.06	5180.04
Wells 1 km	Pipelines 500 m	Pipelines 500 m	Season	12	5201.53	5.28	0.04	5176.53
Wells 1 km	Well pad	Well pad	Season	12	5201.89	5.65	0.04	5176.90
Wells 1 km	Pipelines 1 km	Pipelines 1 km	Season	12	5203.11	6.86	0.02	5178.11
Wells 1 km	Wells 1 km	Wells 1 km	Season	12	5203.29	7.05	0.02	5178.29
Wells 1 km	Road	Road	Season	12	5203.53	7.29	0.02	5178.54
Wells 1 km	Facility	Facility	Season	12	5203.75	7.51	0.01	5178.76
Wells 1 km	Roads 500 m	Roads 500 m	Season	12	5203.82	7.58	0.01	5178.83
Wells 1 km	Aspect	Aspect	Season	12	5203.85	7.60	0.01	5178.85
Wells 1 km	Pipeline	Pipeline	Season	12	5203.94	7.69	0.01	5178.94
Wells 1 km	Roads 1 km	Roads 1 km	Season	12	5204.61	8.37	0.01	5179.62

Wells 1 km	Well years	Well years	Season	12	5204.75	8.51	0.01	5179.76
Wells 1 km	Wells 500 m	Wells 500 m	Season	12	5205.02	8.78	0.01	5180.03

APPENDIX 3.2

Stepwise model selection process for probability of initial occupancy (Ψ), extinction (ε), colonization (γ), and detection (*p*) of bobcats in the Piceance Basin, CO, USA, 2014-2017. The top model is in bold. Predictor variables for *p* included a seasonal effect (Season), which researcher placed the camera (Set by), if the camera was on or off trail (Trail), a model with no variables (Null), if the field of view was partially obstructed or not (FOV), and variation among survey (Survey). Predictor variables for Ψ, ε, and γ included a general model structure which including elevation, aspect and habitat type (General), the number of producing well pads and the density of roads and pipelines within 1km ("Feature type" 1 km) and 500 m ("Feature type" 500 m) of the camera, time since the closest well pad was drilled (Well years), distance to the nearest well pad (Well pad), industrial facility (Facility), pipeline (Pipeline), road (Road), habitat type (Habitat), elevation (Elevation), and aspect (Aspect).

Ψ	ε	γ	*p*	k	AIC*c*	Δ AIC*c*	*w*	Deviance
Step1								
General	General	General	Trail	15	2516.55	0.00	0.60	2485.01
General	General	General	Season	19	2517.32	0.77	0.40	2476.86
General	General	General	Set by	15	2545.42	28.87	0.00	2513.88
General	General	General	Null	14	2546.28	29.73	0.00	2516.94
General	General	General	FOV	15	2548.47	31.92	0.00	2516.93
General	General	General	Survey	37	2568.56	52.01	0.00	2484.86
Step 2								

Wells 1 km	General	General	Season	17	2510.90	0.00	0.11	2474.93
Null	General	General	Trail	12	2511.45	0.55	0.08	2486.46
Wells 1 km	General	General	Trail	13	2511.60	0.69	0.08	2484.44
Null	General	General	Season	16	2511.62	0.72	0.08	2477.87
Wells 500 m	General	General	Trail	13	2511.66	0.76	0.07	2484.50
Wells 500 m	General	General	Season	17	2511.69	0.79	0.07	2475.72
Aspect	General	General	Trail	13	2512.77	1.87	0.04	2485.61
Aspect	General	General	Season	17	2512.84	1.93	0.04	2476.86
Elevation	General	General	Trail	13	2512.98	2.07	0.04	2485.82
Facility	General	General	Trail	13	2513.05	2.15	0.04	2485.89
Roads 500 m	General	General	Trail	13	2513.07	2.17	0.03	2485.91
Well years	General	General	Season	17	2513.12	2.22	0.04	2477.14
Well years	General	General	Trail	13	2513.15	2.25	0.04	2485.99
Roads 500 m	General	General	Season	17	2513.20	2.29	0.03	2477.22
Pipeline	General	General	Trail	13	2513.33	2.42	0.03	2486.17
Habitat	General	General	Trail	13	2513.41	2.51	0.03	2486.25
Roads	General	General	Trail	13	2513.47	2.56	0.03	2486.31
Pipelines 500 m	General	General	Trail	13	2513.50	2.59	0.02	2486.34
Elevation	General	General	Season	17	2513.55	2.64	0.03	2477.57
Roads 1 km	General	General	Trail	13	2513.56	2.65	0.02	2486.40
Pipelines 1 km	General	General	Trail	13	2513.57	2.67	0.02	2486.41
Well pad	General	General	Trail	13	2513.61	2.70	0.03	2486.45

Habiat	General	General	Season	17	2513.69	2.79	0.03	2477.71
Pipelines 1 km	General	General	Season	17	2513.75	2.84	0.02	2477.77
Well pad	General	General	Season	17	2513.75	2.85	0.03	2477.78
Roads	General	General	Season	17	2513.76	2.85	0.03	2477.78
Facility	General	General	Season	17	2513.77	2.87	0.03	2477.80
Roads 1 km	General	General	Season	17	2513.81	2.91	0.02	2477.83
Pipelines 500 m	General	General	Season	17	2513.81	2.91	0.02	2477.84
Pipeline	General	General	Season	17	2513.82	2.91	0.03	2477.84
Step 3								
Wells 1 km	Habitat	Habitat	Season	12	2503.31	0.00	0.13	2478.32
Wells 500 m	Habitat	Habitat	Season	12	2504.03	0.72	0.09	2479.04
Null	Habitat	Habitat	Season	11	2504.22	0.91	0.08	2481.39
Aspect	Habitat	Habitat	Season	12	2505.30	1.99	0.05	2480.31
Wells 1 km	Facility	Facility	Season	12	2505.62	2.31	0.04	2480.63
Null	Facility	Facility	Season	11	2505.95	2.64	0.04	2483.11
Wells 500 m	Facility	Facility	Season	12	2506.05	2.74	0.03	2481.06
Wells 1 km	Habitat	Habitat	Trail	8	2506.37	3.05	0.03	2489.92
Wells 500 m	Habitat	Habitat	Trail	8	2506.55	3.24	0.03	2490.10
Null	Habitat	Habitat	Trail	7	2506.66	3.35	0.02	2492.31
Wells 1 km	Null	Null	Season	10	2506.82	3.50	0.02	2486.12
Wells 500 m	Elevation	Elevation	Trail	8	2506.85	3.54	0.02	2490.40
Aspect	Facility	Facility	Season	12	2506.90	3.58	0.02	2481.90

Wells 1 km	Elevation	Elevation	Trail	8	2506.92	3.61	0.02	2490.47
Aspect	Habitat	Habitat	Trail	8	2507.07	3.76	0.02	2490.62
Wells 1 km	Roads 1 km	Roads 1 km	Trail	8	2507.24	3.93	0.02	2490.79
Wells 500 m	Null	Null	Season	10	2507.29	3.98	0.02	2486.60
Null	Null	Null	Season	9	2507.35	4.04	0.02	2125.91
Null	Elevation	Elevation	Trail	7	2507.39	4.08	0.01	2493.04
Null	Roads 1 km	Roads 1 km	Trail	7	2507.50	4.19	0.01	2493.15
Wells 500 m	Roads 1 km	Roads 1 km	Trail	8	2507.58	4.27	0.01	2491.13
Wells 1 km	Roads 1 km	Roads 1 km	Season	12	2507.89	4.58	0.01	2482.90
Wells 1 km	Facility	Facility	Trail	8	2508.00	4.69	0.01	2491.55
Null	Facility	Facility	Trail	7	2508.02	4.71	0.01	2493.67
Wells 1 km	Elevation	Elevation	Season	12	2508.03	4.72	0.01	2483.04
Wells 500 m	Facility	Facility	Trail	8	2508.15	4.84	0.01	2491.70
Wells 1 km	Null	Null	Trail	6	2508.19	4.88	0.01	2495.93
Aspect	Null	Null	Season	10	2508.28	4.97	0.01	2487.59
Wells 500 m	Null	Null	Trail	6	2508.31	5.00	0.01	2496.05
Null	Null	Null	Trail	5	2508.32	5.01	0.01	2498.14
Wells 500 m	Roads 1 km	Roads 1 km	Season	12	2508.44	5.13	0.01	2483.45
Aspect	Elevation	Elevation	Trail	8	2508.49	5.18	0.01	2492.04
Wells 500 m	Elevation	Elevation	Season	12	2508.53	5.21	0.01	2483.53
Aspect	Roads 1 km	Roads 1 km	Trail	8	2508.56	5.25	0.01	2492.11
Null	Roads 1 km	Roads 1 km	Season	11	2508.62	5.30	0.01	2485.78

Aspect	Null	Null	Trail	6	2508.63	5.32	0.01	2496.37
Null	Elevation	Elevation	Season	11	2508.91	5.60	0.01	2486.07